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PREFACE

The trials and tribulations that attend the preparation, editing, and publishing of the *Annual Review of Entomology* are many, but they are not unbearable. We should be unrealistically insensitive if we did not admit that the rigors of editorship are made almost pleasant by the numerous letters and expressions of encouragement received from readers. Some of these letters have included constructive criticisms, all of which we have given serious consideration. We have already referred to some of these in the Preface to Volume 2. We also explained some of the limitations of publication that prevent us from putting into effect some of the suggestions received.

Among the communications we have received have been inquiries as to how the topics and authors appearing in each volume are selected, and why certain authors and not others are selected. Inasmuch as there appears to be some misunderstanding on this matter, we should like to comment briefly on it here.

To begin with, it must be admitted that the selection of topics and authors is an excruciatingly difficult task. One reason it is so difficult is that entomology is such a diverse branch of biological science, and there are so many capable and talented entomologists, that it would quickly lead us to intolerable frustration if it were not for the fact that we have instituted a sort of "system."

At their annual meeting, members of the Editorial Committee (selected with the confirmation of the Entomological Society of America), plus several invited guests, present their appraisals of the needs for reviews of subjects falling within all of the major branches of entomology. In connection with these appraisals, the numerous suggestions that have come to us during the year are carefully considered. As each topic is selected (and this selection is frequently made after considerable argument, debate, and discussion), potential authors are considered. For most topics, at least three or four entomologists are recommended as possible authors or co-authors. Sometimes the list of capable authors is an extensive one.

The factors involved in selecting, inviting, and obtaining the authors vary. In general, however, the committee strives to select the person most capable of providing us with a review of high quality at the particular time concerned. This person may or may not be one considered by many to be *the* leader in his field, but almost always it is *one* of the recognized leaders in the field. If a particular author who happens to be your idea of the "best" is not the author of a particular review in a particular volume, it may be that your man (*a*) was unable or did not have the time to prepare the review for the particular volume in preparation; (*b*) was invited but declined to prepare the review; (*c*) is being "saved" for a future volume; or (*d*) the Committee has not been advised of his availability. Alternate authors are

usually selected for each topic with the idea of asking one of them to prepare the review if the first author is unable to, or to prepare a review on the same subject for a subsequent volume.

Some fields are so active that it is necessary to review the literature every year, others require reviews every two or three years, and still others require only occasional reviews. Thus, currently very active subjects such as the resistance of insects to insecticides or population dynamics may require more frequent review than slow-moving, but equally important, subjects such as certain basic physiological phenomena or morphological concepts. Moreover, reviews will gradually become current as basic subjects and background material are covered in the early volumes. It is expected that the same subjects will be reviewed in subsequent volumes for which different authors in this field will be invited to prepare reviews. In other words, it is important to remember that the *Annual Review of Entomology* is not a one-volume endeavor. If a leader in a particular field has not yet been invited to write for a particular volume of the *Review*, the chances are that he eventually will be.

Again it is our pleasant obligation to acknowledge the editorial assistance of Mrs. Adele Fumino and others on the staff of Annual Reviews, Inc., as well as the efficient production of the volume by the George Banta Company, Inc.

A.W.A.B. C.D.M.
H.M.H. C.B.P.
R.L.M. R.F.S.
E.A.S.

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THE NERVOUS SYSTEM[1]

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Introduction

The concern of the nervous system in the operation of other organs and indeed of the whole animal make it particularly difficult to select material for a coherent review. The sense organs and muscles are functionally inseparable from the nervous system since they constitute its major input and output. While these organs obviously merit separate reviews, the writer felt that it was necessary to consider nervous input and output, and sections on afferent nerve activity and neuromuscular mechanisms have been included. Current physiological research on the nervous system follows two diverging trends. One of these employs the sensitive techniques of electrophysiology in the exploration of basic neural phenomena; the other seeks to account for the behavior of the whole organism in terms of the organization of its neural units. In spite of its importance the behavioral trend has not been directly considered in this review, partly because the space available would not permit an adequate treatment, and partly because a summary at the present time might be premature. After relative inactivity during the past 15 years, European laboratories have once more taken the lead in this area, and several important studies on the relation of ganglion function to orientation and complex behavior are in progress.

The period of review begins roughly in 1950. For earlier work reference should be made to a survey covering many of the same topics [Roeder (72)]. The organisms covered are limited to insects. This arbitrary limitation is partially justified by the imminent appearance of *Physiology of Crustacea* edited by Waterman (97) in which chapters by Barber, Cohen, Dijkgraaf, Waterman, Welsh, and Wiersma will be particularly relevant. The arthropod nervous system has also been reviewed by Prosser (65) and Crescitelli (18). The finer structure of insect nerve cells, neurochemistry, and neuropathology have been reviewed by Richards (67).

Morphology

A most valuable contribution to insect neuroanatomy has been the magnificent series of papers by Power on the central nervous system of *Drosophila*. In addition to making a detailed study of the distribution of tracts and specific fibers in the brain (54, 56, 57) and thoracico-abdominal nervous system (58), Power examined the effects on the morphology of the nervous system of genetically determined peripheral defects in mutant flies. A reduction or complete absence of ommatidia (55) causes a hypoplasia which is limited to the optic lobes and does not affect the brain. When the com-

[1] The survey of literature pertaining to this review was completed in May, 1957.

pound eye is completely absent the external glomerulus is lacking although the internal glomerulus shows only a 50 per cent hypoplasia. In flightless mutants with normal and with vestigial wings Power (59) could find no morphological evidence of a central nervous defect. Unfortunately, he did not describe the thoracic flight muscles of these insects, but, even if their muscles were completely lacking, the absence of motor nerves might not constitute a very obvious central defect. For reasons given below (see NEUROMUSCULAR MECHANISMS), the motor innervation of even a large muscle mass such as the flight muscle may consist of few fibers and may be morphologically most insignificant compared with a many-fibered sensory nerve. For instance, the sensory nerve from the anatomically small halter is perhaps the largest nerve in the housefly thorax. In his last paper (60) Power showed that the increase in mass of the central nervous system of *Drosophila* follows a smooth sigmoid curve which flattens with cessation of growth about 24 hr. after pupation. However, the neuropile increases logarithmically until the time of emergence while the cortex ceases growth soon after pupation and actually regresses from this point at a rate which compensates for the increase in neuropile. Work such as that of Power is of inestimable value to the neurophysiologist, but it is unfortunate that most neurophysiological techniques are still too crude and clumsy to apply to an insect as small as *Drosophila*.

Fiber connections and the course of tracts within the neuropile remain practically unknown. Vowles (96) applied the technique of ganglion cell destruction and studied consequent fiber degeneration to determine some of the connections of the corpora pedunculata (mushroom bodies) in the brains of the honey bee and various genera of ants. Fibers originating from the small tightly packed cell bodies of the calyces appear to travel no further than the alpha and beta lobes of the corpora pedunculata. Afferent fibers from optic, antennal, and subesophageal sensory centers synapse with these internuncial fibers in the calyces and alpha lobe, while the latter appear to synapse with efferent internuncials in the beta lobe. This appears to confirm the corpora pedunculata as a complex integrating system, but experimental evidence of its mode of operation is lacking.

It has been shown by Goossen (23) [discussed by Rensch (66)] that various members of the Hymenoptera and Coleoptera obey the general rule (Haller's rule) that larger species have a smaller brain to body size ratio than their smaller relatives. On the other hand, in larger species the corpora pedunculata are larger in proportion to the overall brain size, their structure is more complex, and the number of cells in the calyces is greater.

It is unfortunate that most of the excellent descriptions of insect musculature [e.g. Carbonell (8)] do not also supply information on innervation. Nijenhuis & Dresden (51, 52) have partially rectified this with studies of the topographic anatomy of the muscles, sense organs, and motor nerves of the mesothoracic leg of *Periplaneta americana* (Linnaeus). They have also (21) related muscle and joint anatomy to motion in the mesothoracic leg. A topographic study of nerves, muscles, and sense organs in the neck region is con-

tained in the work of Mittelstaedt (50) on head movements and gravitational sense in *Anax imperator* Leach, while a detailed study by Wittig (104) of the morphology of the thorax of *Perla abdominalis* Burmeister contains much valuable information on nerve distribution and sensory structures. The cytology of insect neurons as revealed by supravital methylene blue staining has been studied by Meyer (49).

Wigglesworth (102) has shown that new sensory neurons continue to differentiate from ordinary epidermal cells throughout the nymphal development of *Rhodnius prolixus* Stål. Following cauterization of a cuticular area the axons growing out from newly regenerated sense cells appear to follow any nerve they encounter and travel centripetally along it. Sometimes their growing tips curve so as to encounter a loop of the same or of other axons regenerating from the same region, a circumstance which may trap them in a closed loop or "circular nerve" composed of hundreds of fibers. Nerve regeneration in nymphs and adults of *Periplaneta* is apparently much more extensive than is generally recognized. According to Bodenstein (4), there is extensive axon regeneration from central and peripheral stumps of severed metathoracic nerves and even from the connectives after removal of the entire metathoracic ganglion. Although motor fibers may reinnervate muscles (as revealed by a return of their excitability to electrical stimulation) even from a ganglion transplanted into the coxa, extensive interruption of a nerve pathway always results in regeneration of an anomalous nerve pattern and functional reflex communications are not re-established.

Nerve Activity and Impulse Transmission

Giant fiber systems.—An ascending group of four large (8 to 13 μ) fibers has been described by Cook (16) in the abdominal nerve cord of *Locusta migratoria* Linnaeus. These fibers appear similar in distribution and function to the giant fibers of *Periplaneta* [see Roeder (72)] although they are smaller in diameter and fewer in number. The largest could be traced to a single cell body at the posterior end of the last abdominal ganglion, and all appear to serve as internuncials between the cercal nerves and thoracic motor centers. Air puffs on the cerci elicit electrical responses in giants and motor fibers although evasive behavior corresponding to that found in *Periplaneta* was not observed in *Locusta*. The largest nerve fibers in the abdominal nerve cord of *Anax imperator* nymphs appear to fall into the same category. Hughes (42) has shown that these *Anax* giants give off collaterals in the neuropile of abdominal ganglia in addition to terminations in the thoracic ganglia. Excitation of the system causes folding of the legs and contraction of the abdominal musculature which streamlines the animal and expels water from the rectum for the jet propulsion by which dragonfly nymphs evade predators. The afference of this system has not been located although it appears to be abdominal.

Spiracular nerves.—Case (10) has provided experimental evidence that the right and left spiracles of a segment of *Periplaneta* and *Blaberus* have a

common innervation from each of two motor axons which leave the corresponding ganglion by the median nerve and bifurcate in the transverse nerves. Closure of the thoracic spiracle may be elicited by mechanical stimulation of adjacent hair sensilla whose afferents enter the succeeding ganglion. Spiracular opening is caused by high CO_2 and low O_2 tension [Case (9); Schneiderman (83)] acting at some unknown locus, possibly in the central nervous system.

Ganglion activity.—The dense matrix of interwoven fibers composing the neuropile has defied any attempts to obtain a clear picture of the morphology of insect synapses, and there is little recent progress in clarifying the details of synaptic transmission through specific pathways. However, such information is urgently needed if we are to provide a neural basis for reflexes and behavior. Hughes (40) found that direct current passed at different intensities and in different directions through the metathoracic ganglion of *Periplaneta* evokes patterned rather than mass responses in the leg muscles. He considers the possibility that the form and magnitude of naturally occurring three-dimensional potential fields within the neuropile are modified by impulse inflow, the form of patterned movements being determined by the arrangement of internuncials within these changing fields rather than by transmission along "closed" tracts linked by synapses. A similar hypothesis could be based on changing local concentrations of a mediator (see *The cholinergic system*) but the whole matter must remain highly speculative until we have more precise information about the finer structure and the local electrical and chemical events in the neuropile. The degeneration technique employed by Vowles (see above MORPHOLOGY) when combined with electrophysiological exploration using microelectrodes and with behavioral studies may throw some much needed light on this important question.

Real progress in revealing the details of synaptic transmission in an insect ganglion has been made by Hagiwara & Watanabe (27). They examined the reflex pathways for excitation of the tymbal (sound-producing) muscle of the cicada, *Graptosaltaria nigrofuscata* Motschulsky. Each muscle is innervated by a single motor fiber whose cell-body lies in the caudal region of the fused meso- and metathoracic ganglia. Indirect excitation of these motor neurons was accomplished by stimulation of an abdominal nerve of unstated distribution. A single shock of increasing intensity elicited a regular sequence of from one to seven spikes in each motor nerve. The frequency of the discharge was 100/sec., and the discharge in right and left motor fibers showed precise alternation when either afferent nerve was stimulated. Estimated conduction times were; afferent time, 10 to 20 msec.; central reflex time in the ganglion, 30 to 40 msec.; motor nerve time, 3 msec.; neuromuscular time, 6 msec.

For the first time in insects Hagiwara and Watanabe were able to record the membrane potential changes from the interior of a motor neuron soma by means of a microelectrode. The resting potential was 60 mv. In spite of the fact that these motor neurons are presumably monopolar and the soma is

probably not in the direct conduction path, a typical prepotential and an overshoot in the action potential (75 mv.) was recorded. The regularity of the motor discharge and the precise alternation of spikes in the right and left units is apparently controlled by a premotor pacemaker mechanism, for which some evidence is presented. Interposition of a supernumerary spike by antidromic stimulation in the midst of a regular sequence of reflex origin failed to upset the rhythm and merely caused a compensatory pause.

The closeness of coupling or degree of interaction between synapsing neurons may vary at different points in the same reflex pathway, the lability of a reflex depending upon the most labile synapse [Roeder (69, 70)]. Many sense cells and central neurons are spontaneously active, and impinging stimuli or presynaptic impulses may serve merely as modulators of the spontaneous rhythm. Roeder (73) discusses the origin and significance of spontaneous activity in relation to excitability and reviews the evidence that spontaneous activity of central neurons may play a significant part in certain forms of behavior. Thus, the pattern of effective sexual activity released in the praying mantis after decapitation coincides with, and may be partly the result of spontaneous activity in motor neurons of the phallic motor system [Roeder (74)]. Weiant (99) has shown that spontaneous activity of motor neurons in the metathoracic ganglion of *Periplaneta* is inhibited bilaterally by ganglia in the head and contralaterally by elements in the opposite half of the same ganglion.

Afferent nerve activity.—The pattern of nerve impulses in sensory fibers is a valuable source of information on the potentialities of a sense organ. It is also the input in coded form of the external world to the central nervous system. For the latter reason a review of the nervous system cannot disregard afferent nerve activity, although no attempt will be made here to summarize information on sensory physiology.

The rapid adaptation shown by certain mechanoreceptors has been given new significance by the work of Pringle & Wilson (64). They applied a sinusoidal low-frequency deflection to a single femoral spine on the leg of *Periplaneta* and observed the phase relations between response frequency and bending. Owing to adaptation of the end-organ maximum impulse frequency precedes maximum mechanical displacement of the spine by 45 degrees. They pointed out that this tendency of impulse frequency to lead displacement must in some measure counteract the time lost through conduction in a reflex response. If such a receptor were the sensing element in a closed feedback loop envolving the maintenance of posture this anticipatory characteristic would add stability to the system by counteracting the delay imposed by the reflex time. While insect proprioceptors commonly include nonadapting or slowly adapting elements to which this argument would not apply, they also include rapidly adapting elements responding only to phasic activity.

Mechanoreceptors are concerned in spiracle closure in *Periplaneta* [Case (10)] and afferent discharges occur during the respiratory movements of

Dytiscus and *Locusta* [Hughes (41)]. Certain afferent fibers in *Locusta* discharge both during respiratory movements and during stimulation with low-frequency sounds, and Hughes concluded that chordotonal organs are implicated. Finlayson & Lowenstein (24) report that sensory neurons sensitive to stretch are found in the intersegmental muscles of Lepidoptera. Until the present, insect proprioceptors were thought to be limited to the cuticle.

The effect of artificial sounds and natural stridulation upon the afferent discharges from tympanal organs, cercal sensilla, and receptors on abdominal and thoracic sclerites were compared by Haskell (28) in four species of Acrididae. In these forms the cercal sensilla appear to play little part in natural air-borne sound reception, but sensilla on abdominal pleura and sternites may augment the tympanal organs at higher sound intensities. The random variability of the sound pattern of successive stridulatory pulses and of the spike pattern in the tympanic nerve of the recipient lead Haskell to conclude that there is no evidence of a peripheral mechanism for discriminating the species-specific songs of these insects beyond the pulse repetition frequency. However, this conclusion requires confirmation through an examination of single unit responses in the tympanic nerve and in second-order units in the ganglion.

Afferent impulses from the tympanic organ of phalaenid moths were recorded by Haskell & Belton (29). Treat & Roeder (76, 92) showed that the acoustic response in phalaenids is mediated by two receptor units which differ in relative acoustic sensitivity. These acoustic units discriminate intensity but not pitch over a frequency range of 3 to more than 100 kc./sec. and are particularly adapted to receive pulsed sounds such as those made by echo locating bats. In addition to the two acoustic fibers the tympanic nerve contains a third acoustically insensitive but spontaneously active unit. Although the frequency of the latter is altered by mechanical distortion of the ear its function is unclear.

The smaller fibers and generally close grouping of chemoreceptor units have made it somewhat more difficult to get a clear picture of their input to the central nervous system. Hodgson, Lettvin & Roeder (30) used a pipette electrode containing the stimulant chemical to record the responses of single chemoreceptive hairs on the labellum of flies. Results obtained with this method [Hodgson and Roeder (31)] are in accord with those of Dethier (19, 20) from extensive behavioral studies. Each chemosensory hair contains the processes of two neurons which extend to a minute area at its tip. That unit producing the larger spike responds with a series of impulses when compounds which elicit behavioral rejection are applied to the sensory area. The other unit responds with a smaller spike to compounds which elicit behavioral acceptance. Both units show adaptation, a tendency to spontaneous activity, and a response to bending of the hair. Thus, discrimination of acceptable and unacceptable compounds appears to depend upon a peripheral mechanism.

The input from single olfactory receptors has been harder to identify.

Roys (79) recorded bursts of impulses from afferent nerves in the antennae and legs of cockroaches exposed to concentrations of benzene vapor capable of producing avoiding reactions in the intact insect. He concluded that this response might be associated with a common chemical sense involving non-selective excitable tissue, and suggested that receptors mediating responses to behaviorally significant odors might differ only in the possession of special filter-like mechanisms. Schneider & Hecker (81, 82) inserted capillary electrodes into the antennae of male *Bombyx mori* (Linnaeus) and recorded changes both in spike frequency and in slow potentials when a rod bearing the sex odor of female moths or cycloheptanone was brought near to the antennae. No response was obtained from the antennae of female moths. Boistel, Lecomte & Coraboeuf (7) recorded changes in spike frequency from the antennae of wasps and bees exposed to various essential oils. Winter bees are much less sensitive than summer bees, and 5 per cent carbon dioxide facilitates the response.

The unstabilizing effect of DDT on receptor cells in insects [Roeder & Weiant (77)] suggested to Hodgson & Smyth (32) the possibility of using a local application of DDT to a sense cell as a marker for tracing the course of its afferent fiber in compound nerves and in the central nervous system because of the characteristic impulse trains present therein. Using *Sarcophaga* they followed the spread of DDT within the body by this means. The neural instability induced by DDT poisoning may actually amplify the sensitivity of sense cells by increasing their tendency to repetitive discharge on natural stimulation. Smyth & Roys (87) found that the early effects of DDT on sense cells was to increase the afferent discharge and to lower ninefold the sucrose acceptance threshold in houseflies and blowflies, although it had no effect on rejection thresholds. The acceptance thresholds of DDT-resistant houseflies are unaffected by DDT treatment and Weiant (98) has demonstrated that their receptors show only transitory instability or no effect when exposed directly to the action of DDT.

Neuromuscular Mechanisms

Locomotion.—Economy of motor nerve fibers is associated with special mechanisms for securing a wide range of contraction patterns in the muscle of Crustacea [Wiersma (100)] and insects. Study of these mechanisms in insects has been aided by the anatomical and functional work of Carbonell (8), Nijenhuis & Dresden (51, 52), Dresden & Nijenhuis (21), and Hoyle (36) on the thoracic segments of the cockroach and locust. Nervous control of insect muscles has been reviewed by Hoyle (39).

The *extensor tibialis* muscle of the cockroach is supplied by two types of nerve fiber, one producing quick powerful twitches and one producing slow shortening of the facilitatory type [Pringle (61)]. In a series of important papers Hoyle and his associates have provided a fairly complete picture of the operation of this system in the *extensor tibialis* muscle in the metathoracic leg of the locust, *Locusta migratoria migratorioides* Reiche and Fairmaire.

The *extensor tibialis* is the main source of propulsion when the locust jumps, at which time this muscle may develop the considerable tension of 20,000 grams per gram of muscle [Hoyle (37)]. At other times it is capable of slow and gentle contractions when the locust walks. The *extensor tibialis* is supplied by a motor nerve fiber of the "fast" type (F) via nerve 5, and two fibers of the "slow" type (S_1 and S_2) via nerve 3b. The F nerve fiber sends branches to all of the *extensor tibialis* muscle fibers. As each branch approaches a muscle fiber it divides further into a series of twigs terminating in motor endings distributed 50 to 100μ apart over the full length of the muscle fiber [Hoyle (36)]. A similar profusion of motor endings has been observed by earlier workers [see Roeder (72)].

Jumping in the locust is accomplished through a single impulse or short impulse train in the F fiber, eliciting a twitch or short tetanus. If the F fiber is severed the locust is unable to jump, but can still make walking movements which are controlled by the S_1 fiber [Hoyle (37)]. This motor unit supplies only about 30 per cent of the *extensor tibialis* fibers. Single S_1 impulses produce either no contraction or minute twitches. Ultimate tension is a function of S_1 impulse frequency from just detectable shortening at 10/sec. to one quarter of the F tension at 150/sec. Relaxation is immediate following cessation of S_1 stimulation. Thus, interplay of F and S_1 appear to account for the range of speeds and tensions of which this muscle is capable. S_2 will be considered below.

This system, consisting of two dissimilar and partially over-lapping motor units, receives no obvious explanation from a comparison with the system of multiple parallel all-or-none motor units which compose most vertebrate muscles. An answer lies in the difference in the distribution of motor endings and in the mechanism of neuromuscular excitation. The arrival of a motor nerve impulse at a vertebrate motor end-plate generates an intense local electrical depolarization (end-plate potential or e.p.p.). The e.p.p. has a negligible effect on the contractile mechanism and serves mainly as an ion leak or resistance drop for the generation of the active muscle membrane response (muscle action potential or m.a.p.) which sweeps in all-or-none fashion in both directions from its single point of origin to activate the contractile mechanism.

Unlike the phasic skeletal muscle fibers of vertebrates which depend upon detonation by the e.p.p. at a single point of nerve-muscle contact, insect muscle fibers make contact with the motor nerve at many points [Hoyle (36); see also Roeder (72)]. This led to the suggestion [Roeder & Weiant (77)] that excitation of certain extrinsic leg muscles in the cockroach, *Periplaneta americana*, might depend entirely upon a series of local and possibly overlapping depolarizations analogous to e.p.p.'s. Assuming that these local depolarizations triggered corresponding small local contractions, total muscle shortening could be accomplished by series summation of the local contractions and without the intervention of m.a.p. One function of the m.a.p., that of transmission over the whole fiber, would thus be accomplished by the motor

nerve impulse. A very similar situation has been suggested for the muscles of Crustacea [Wiersma (100); Prosser (65)]. The absence of a propagated m.a.p. in the tergal remotor muscle of the cockroach is further suggested by the observation [Roeder and Weiant (77)] that this muscle becomes inexcitable to direct stimulation within a few days after the motor nerve has been severed surgically and allowed to degenerate.

More precise information regarding this hypothesis has been obtained by recording potentials from microelectrodes placed on, or inserted within single muscle fibers. In the *extensor tibialis* of the cockroach [Wilson (103)] and locust [Hoyle (37)] the resting muscle membrane potential of single fibers averages 60 mv. Stimulation of the F nerve fiber brings this membrane potential nearly or quite to zero, only occasionally causing a reversal of sign. The major initial portion of this depolarization appears to be due to an event analogous to the vertebrate e.p.p., while a smaller terminal portion is considered by Hoyle (37) to be an active muscle membrane response. However, active propagation along the muscle membrane does not come into question since the same end is accomplished by the sequential but almost simultaneous development of local depolarizations over the length of the fiber. A similar situation has been found in the *flexor tibialis* of the locust [del Castillo, Hoyle & Machne (11)], the flight muscles of the locust, and under certain circumstances in the tymbal muscle of the cicada, *Platypleura kaempferi* (Fabricius) [Hagiwara (25); Hagiwara & Watanabe (26)]. In the latter case the muscle potential showed a greater overshoot, which suggested to the authors that a propagated potential plays a greater role in excitation. The cicada tymbal muscle will be discussed later. The tension developed in the locust *extensor tibialis* to an F tetanus is many times higher than that produced by a single F impulse [Hoyle (37)]. Therefore, either the local muscle depolarizations or the local contractions produced thereby are subject to some form of temporal facilitation.

The electrical response of the locust *extensor tibialis* fibers to impulses in the S_1 fiber is of great interest [Hoyle (37)]. Of those muscle fibers (30 per cent of the total) innervated by S_1 about one third receive endings (S_{1a}) which generate a slow graded depolarization showing facilitation. The other two-thirds of the fibers innervated by S respond to nerve stimulation by small (4 to 30 mv.) brief and variable e.p.p.'s (S_{1b} endings) accompanied by small twitches of the innervated fibers and possibly by small local membrane responses. S_{1b} can generate the equivalent of one quarter of the F tetanus tension. The important point is that S_1 tension, in contrast to F tension, develops as a slow smooth contracture (S_{1a}) at low frequencies with superimposed local twitches and tetanus (S_{1b}) at higher frequencies. These effects would account for postural tonus and for the gentle phasic activity of walking. Eighteen per cent of the fibers of the cockroach *flexor tibialis* penetrated by a microelectrode gave rise to similar small (8 to 20 mv.) and slow potential changes which showed a marked facilitation [Wilson (103)]. Other muscles of the locust appear to be similarly controlled [Hoyle (37)]. The *flexor tibialis*

of the cockroach [Wilson (103)] and locust [Hoyle (37)] may, in addition, be subdivided into a small number of separate motor units.

This situation is similar to that found in Crustacea [Weirsma (100)] with the exception that no neuromuscular inhibitory nerve fiber has been demonstrated in insects. The S_2 fiber innervating the *extensor tibialis* of the locust produces no mechanical change when stimulated alone, nor does it show any subtractive or additive effect when stimulated in combination with F and S_1 [Hoyle (37)]. In contrast with the inevitable depolarization produced by F and S_1, S_2 has a hyperpolarizing action on fibers having a low membrane potential, raising the latter from 50 mv. to as much as 70 mv. during repetitive stimulation. In this respect S_2 resembles the inhibitory fiber of the Alexandrowicz proprioceptor in Crustacea [Kuffler & Ezyaguirre (44)]. However, since there is a proportional increase in the depolarization produced by F fiber stimulation during S_2 stimulation, no effective inhibitory action is produced. A similar result follows hyperpolarization with an external source of e.m.f., and Hoyle (37, 38) concludes that S_2 serves rather to raise the membrane potential and local response in fibers partially depolarized by increased blood potassium after the insect has eaten large amounts of plant tissue. S_2 would enhance rather than inhibit the muscle response under these conditions.

Flight.—Wingbeat frequencies of 150 to 300 per second are characteristic of many flies, bees, and wasps, and short bursts of thoracic vibration at 2200 per sec. have been recorded [Sotavalta (88)] in a small midge after amputation of the wings. Since nerve excitation in the muscles discussed in the previous paragraphs produces a tetanus at stimulus frequencies higher than 30 to 50 per sec., these high wingbeat frequencies suggest other factors in the excitation of the indirect flight muscles.

Pringle (62) was the first to demonstrate that in *Calliphora* muscle potentials recur asynchronously and at a much lower frequency than the wing movements. This potential-movement asynchrony and a relatively high wingbeat frequency were found [Roeder (71)] to be characteristic of Diptera, Hymenoptera, and Coleoptera. Synchrony and a generally lower wingbeat frequency were found in Lepidoptera, Orthoptera, and Odonata. The Homoptera and Hemiptera are possibly intermediate and may possess both types of movement [Pringle (63); Teigs (91); Boettiger (5)]. Pringle (62) suggested that the wingbeat rhythm in "asynchronous" forms is myogenic, occurring only when the muscle units are brought into an appropriate state by motor nerve activity. Boettiger, Furshpan, and collaborators in a series of papers [reviewed by Boettiger (5)], have demonstrated in bumble bees, flies, and wasps that both vertical and horizontal indirect flight muscles are in a sustained tetanus during flight. This tetanus is maintained by neuromuscular excitation and accompanied by conventional membrane changes as measured with intracellular microelectrodes (membrane potentials, about 60 mv. action potentials 80 to 100 mv.). A muscle oscillation which drives the wingbeat is superimposed upon this tetanus. The ability of the flight muscle to oscillate

at a frequency other than that of the activating nerve impulses appears to be the result of an intrinsic mechanism reversing the active state during the cycle so that tension is highest during shortening and lowest during lengthening of the muscle. This could be described as a shift in phase between tension and length, tension changes leading length changes during the work cycle of the activated muscle. The oscillation is present only when an activated muscle has a load possessing inertia or its equivalent, and its frequency varies with load and with the elastic constants of the system. In Diptera there is evidence [Boettiger & Furshpan (6)] that the oscillation of the activated indirect flight muscles is transmitted to the wings via a mechanical quick-release or click mechanism envolving various thoracic sclerites. Under isometric conditions the activated flight muscle behaves in a conventional manner. A similar deactivation or sudden drop in tension immediately following a quick release during an isometric tetanus has been postulated by Pringle (63) to explain the operation of the tymbal muscle of certain cicadas which drives the tymbal at a much higher frequency than that of the motor nerve impulses. The basis of this curious characteristic of fibrillar muscle is not known, but since it concerns the physiology of muscle rather than of nerve it will not be pursued further.

Spiracular muscles.—The occlusor muscles of the spiracles show still another pattern of activity. Case (10) has found that following motor nerve section these muscles go through various phases of excitability until a state of fasciculation is reached which lasts, together with excitability to direct stimulation, for as long as 3 months. The denervated spiracular muscle of the cecropia moth pupa [Schneiderman (83)] and the cockroach [Case (10)] continues to relax (spiracular opening) in high CO_2 and low O_2 tensions although this response in the cockroach is much less sensitive after the elimination of central nerve connections.

Chemical Factors in Nerve Activity

The cholinergic system.—The powerful neurotoxic action of nicotine on insects has long suggested that important phases of synaptic transmission in the central nervous system are cholinergic in nature. Earlier studies [see Roeder (72)] of the action of anticholinesterases on spontaneous nerve activity and synaptic transmission supported this idea, although the lack of action of cholinergic blocking agents and of acetylcholine on junctional processes suggested a contradiction. However, recent work providing more precise identification of the components of the cholinergic system in the insect nervous system and on the properties of the sheath which surrounds it has done much to confirm the importance of acetylcholine in insect nerve function.

Following indications of acetylcholine-like substances in insect tissue [Corteggiani & Serfaty (17)] three groups of workers have provided unequivocal identification of acetylcholine. Lewis (45) applied the methods of bioassay and chromatography to insect tissues; Augustinnson & Grahn (1) used

similar techniques plus chemical isolation with honey bee heads; Chefurka & Smallman (14, 15) used chromatography, electrophoresis, bioassay, and chemical methods to identify acetylcholine in house-fly heads.

Although acetylcholine was demonstrated in each case, the methods of extraction and identification resulted in considerable losses and a small yield. Lewis & Smallman (46) compared various technical procedures and concluded that acid extraction and boiling of heads followed by bioassay gave a maximum of acetylcholine. Their results (in μg./gm.) were as follows: *Calliphora* heads 32.7, *Lucilia* heads 28.3, *Musca* heads 26.1, *Tenebrio* heads, 7.8, *Periplaneta* heads 9.8, *Periplaneta* nerve cords 36.7. If the fly brain contains most of the acetylcholine found in the head then it is certainly one of the richest sources of acetylcholine.

Rapid synthesis of acetylcholine in extracts from *Lucilia* adults was noted by Lewis (45). The details of this process in *Lucilia* heads have now been revealed by Smallman (84). The first step is the formation of acetyl coenzyme A from separate enzyme systems utilizing either citrate or acetate; the second is the acetylation of choline catalysed by choline acetylase. When the first step is not the limiting factor the second occurs at an exceedingly high rate, an observation which conforms with the high acetylcholine content recorded above. Winteringham & Harrison (101) prevented the destruction of acetylcholine in fly heads and thoraces by injection of DFP and followed its formation by injecting C^{14} labeled acetate. The amount of extractable acetylcholine doubled during the first 30 minutes of poisoning but returned to normal levels during the ensuing 5 hours.

The other essential component of a cholinergic system, cholinesterase, has been found by many workers in the nervous systems of a variety of insects. Although its activity in some forms is very high, this may vary greatly with the habits and activity of the species [Metcalf, March & Maxon (47)] and may drop to zero during periods of inactivity such as diapause [Van der Kloot (95)]. While much of this activity is due to a true or specific acetylcholinesterase, particularly in highly active insects [Wolfe & Smallman (105)], acetyl-B-methylcholine and a variety of aliphatic esters may also be hydrolyzed by breis of bee, fly, and cockroach heads [Babers & Pratt (2, 3); Metcalf, March & Maxon (47)]. An aromatic esterase predominates in the body tissues of the cockroach and honey bee. It is relatively insensitive to the action of organophosphates and may play a part in the detoxification of these agents [Metcalf *et al.* (48)]. The pH, temperature, and salt concentrations favoring optimum activity of acetylcholinesterase from fly and bee heads have been determined by Chadwick, Lovell & Egner (12, 13) and Wolfe & Smallman (105). Homogenates from these sources contain the enzyme both in particulate and in soluble form and this phase distribution is influenced by salts and pH [Smallman & Wolfe (86)]. Kearns (43) has reviewed recent work on the inactivation of insect cholinesterases by organophosphates.

Correlation of the presence of these cholinergic components with activity

in the nervous system has not been quite so clear although some progress has been made. Van der Kloot (95) has shown that at the onset of pupation and during subsequent diapause the brain of *Hyalophora cecropia* (Linnaeus) loses all spontaneous nerve activity and electrical excitability and its cholinesterase content falls to zero. These conditions persist throughout diapause during which an acetylcholine-like substance accumulates steadily in the brain tissue. After chilling the pupa and within a few days before the onset of adult development there is a reappearance in the brain of cholinesterase, electrical activity, and neurosecretory activity, while the acetylcholine-like substance drops to a low level. These changes are limited to the brain, cholinesterase and neural activity remaining unchanged in the nerve cord during diapause. Similar changes were not detected in the brain of *Galleria*, which does not show a pupal diapause. Acetylcholine increases in the heads of house flies during the early (spasmodic) phase of poisoning with organophosphorus compounds [Winteringham & Harrison (101); Smallman & Fisher (85)]. Rockstein (68) has shown that although there is a steady decrease in the number of nerve cells in the brain of the adult honey bee during the process of aging the cholinesterase content remains relatively unchanged after an initial rise during the first week of adult life.

The action, or rather, the lack of action of external acetylcholine on the insect nervous system has been partially accounted for. Hoyle (33, 35, and see below) showed that the sheath surrounding the central nervous system and major nerves of *Locusta migratoria* may act as an effective barrier to potassium ions. Twarog & Roeder (93) described a technique whereby the sheath may be removed from connectives and ganglia of *Periplaneta americana* without alteration in axonic or synaptic transmission. Acetylcholine $10^{-2}M$, which is without action on intact ganglia, causes a rapid but reversible synaptic block when applied after desheathing. After pretreatment with eserine acetylcholine 10^{-3} to $10^{-4}M$ produces reversible block in desheathed ganglia. Twarog & Roeder (94) have also examined the effects of a number of other pharmacological agents and substances of biological origin on desheathed ganglia and axons of the cockroach.

In spite of this increase of one hundredfold or more in the effectiveness of acetylcholine applied after desheathing, the sensitivity of insect synapses to acetylcholine is still low when compared with many other cholinergic systems. This suggests that other physical or chemical obstructions may surround synaptic areas at deeper levels of the nervous system. In an examination of the synaptic action in *Periplaneta* of a series of organophosphates of high anticholinesterase potency Roeder & Kennedy (75) considered the possibility that these compounds might be exerting a double action—an irreversible inhibition of cholinesterase at low concentrations and a reversible competition between agent and mediator for available receptor substance at higher concentrations. Insect synapses may operate in a relatively closed local environment containing a steady and possibly high ambient concentra-

tion of acetylcholine, and a post-synaptic impulse may be evoked only when the level of ambient acetylcholine becomes critical through increments of pre-synaptic origin. On this basis low concentration gradients as well as diffusion barriers might explain the relative ineffectiveness of externally applied acetylcholine.

In addition to this evidence for the presence of a cholinergic system in insects there are indications of the presence of other active substances in the insect nervous system. Lewis (45) noted an active substance in extracts of DDT-poisoned *Calliphora* which did not appear to be acetylcholine. Augustinnson & Grahn (1) found two other unidentified esters in honey bee heads. Ostlund (53) showed that insect neural tissue contained epineprhine and nor-epinephrine, and Twarog & Roeder (94) found that these neurohumors were more effective than acetylcholine on synaptic transmission in *Periplaneta*. Other types of esterase have been identified also (see above) although there is no indication of their functional significance. Sternburg, Chang & Kearns (89, 90) have reported that a neurally active substance appears in the blood of *Periplaneta* and other arthropods after poisoning with DDT or exposure to repeated electric shocks. It appears to be distinct from DDT, acetylcholine, epinephrine, nor-epinephrine and histamine, and does not inhibit cholinesterase. In low concentrations it causes a marked increase in the spontaneous electrical activity of isolated nerve cords of the roach, but in higher concentrations it may block all nerve activity.

Potassium and sodium.—The importance for nerve impulse transmission of fixed relative concentrations of these ions in the external medium and the fact that their ratio may fluctuate widely in insect hemolymph are widely recognized [see Roeder (72)]. This paradox was partially resolved by Hoyle (33) who showed that while the intact crural nerve of the phytophagous insect *Locusta migratoria* maintains conduction for several hours in saline containing 70 m*M* KCl, the same solution injected below the sheath blocks conduction within 10 sec. The effect of potassium on the muscle membrane potential [Hoyle (34)] suggests that this block is due to a depolarization similar to that known for crustacean and vertebrate axons. This indicates that the sheath surrounding the central nervous system and larger nerves provides an effective barrier or regulator for potassium fluctuations in the hemolymph. The tracheal membranes surrounding muscles appear to be a much less effective barrier to such changes, and Hoyle (34, 35) has shown that following a plant meal the high potassium content of the blood may partially depolarize the muscles of the locust without appreciable interference with nerve impulse conduction. Since the insect muscle membrane does not play an essential part in the spread of excitation over the muscle fiber (see NEUROMUSCULAR MECHANISMS) its partial depolarization by potassium does not result in all-or-none neuromuscular block but merely reduces the maximum twitch tension and tonus and hence the activity of the insect [Hoyle (38)]. Hoyle (35) has shown that starvation may reduce the potassium content of

locust hemolymph by 50 per cent. This causes an increase in twitch height and tonus and, through proprioceptive feedback, the general excitability of the insect. Ellis & Hoyle (22) provide evidence that a low blood potassium is one of the factors determining the onset of marching behavior in locusts. Marching may be retarded by a meal of filter paper soaked in sugar solution only if potassium chloride is also added.

Removal of the sheath from the abdominal connectives and ganglia of *Periplaneta americana* was accomplished by Twarog & Roeder (93). In the saline used by Hoyle (34) conduction in the desheathed giant fibers was unimpaired although the blocking time of, and recovery from, 140 m*M* potassium was shortened from 25 min. to 1 to 2 min. Sodium-free (sucrose substituted) saline sustained giant fiber conduction indefinitely in the intact cord although it blocked within 30 sec. in desheathed preparations. In contrast to potassium and sodium, water passes readily through the sheath. However, the mechanical toughness of the sheath appears to prevent appreciable swelling in hypotonic saline and may serve an osmoregulatory function.

The mechanical properties of the sheath [the perilemma of Scharrer (80)] appear to depend upon a tough outer neural lamella which is devoid of cellular structure. Below this is a layer of squamous epithelial cells termed the perineurium [Scharrer (80)] or perilemma [Hoyle (33)]. The demonstrated role of the sheath in ion regulation of the central nervous medium raises the important question of the route by which glucose and other metabolites reach the central neurones, and it must be considered in future work on insect pharmacology, toxicology, regulation, and intermediary metabolism.

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CHEMORECEPTION IN ARTHROPODS[1]

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The term "chemoreception" designates the physiological processes occurring in certain receptor cells as a result of their contact with chemical stimuli. The significance of these processes for entomology derives from the fact that they trigger a great variety of the most important behavior patterns of insects, including feeding behavior, habitat selection, host-parasite responses, and behavior integrating caste functions among social insects. Chemoreception also mediates the responses of insects to attractants, repellents, and some insecticides.

In the extensive literature documenting studies on this sensory system of insects, two trends are apparent. The first of these has been characterized by an empirical approach arising from immediate needs to find chemicals which modify the behavior of insect pests in predictable ways. The second, a more orderly scientific approach, has been directed toward building a conceptual framework concerning the basic physiology of chemoreception. Since the latter trend, in the long run, promises to be the more productive, both for applied work and as a contribution toward understanding the general biology of insects, it will be the approach treated most extensively in this review.

The systematic analysis of behavior mediated by chemoreception has undergone progressive refinement during the past decade. Many earlier studies consisted of relatively simple description of the gross morphology of sense organs and the behavior of insects under partially controlled conditions. At that time the exact functions of any receptor cell could only be inferred, even after the most detailed histological descriptions. Frings & Frings (1) and Dethier & Chadwick (2) have reviewed the most important of these earlier observations. Similar literature dealing with invertebrate animals in general has been reviewed by von Buddenbrock (3), Hogdson (4), and by Jahn & Wulff (5).

In 1947, using a technique which had been introduced by Minnich (6), Dethier & Chadwick began the most extensive series of tests yet performed concerning the relationship between molecular structure and stimulating effectiveness of chemicals acting upon chemoreceptor cells. In their tests the important variable of nutrition was controlled, statistically significant populations were studied, some isolation of central and peripheral nervous processes was achieved, and a new standard of refinement was established for studies on chemoreception. The results have been summarized by Dethier (7, 8). In 1945, the first studies on the functions of individual primary chemoreceptor cells were reported by Hodgson *et al.* (9) and by Schneider (10). Both these studies utilized electrophysiological techniques similar to

[1] The survey of literature pertaining to this review was completed in April, 1957.

those which had been previously used by neurophysiologists in the study of other sensory systems. Since it became apparent that much of the behavior of certain intact insects could be accurately predicted from a determination of functions in single chemoreceptor cells, there is at the present time a rapidly increasing emphasis upon direct study of the physiology of primary chemoreceptor cells, using electrophysiological techniques. The methods and results of this type of analysis have not been extensively reviewed heretofore, and it seems appropriate that they should be described in some detail at this time. Moreover, with the extension of analyses of chemoreception to a cellular level it is apparent that findings on arthropods other than insects have much to contribute to the development of the physiological concepts, and consequently the relevant studies on arthropods in general will be included in this review.

The refinements of technique which make it possible to experiment with more precisely localized components of the chemosensory process also impose the need for a precise use of terms to designate the structures and processes studied. For example, now that it is possible to study the functions of individual chemoreceptor cells, it is obviously desirable to maintain a rigorous distinction between the "chemoreceptor cell" and the "sense organ"—both of which have sometimes been designated in earlier literature by the ambiguous term "receptor." The ultimate interest in any analysis of chemoreception is the actual chemoreceptor cell. The other parts of the sense organs are chiefly of concern only to the extent that they amplify or filter out stimuli reaching the chemoreceptor cells, or may influence the receptor cell activity in other ways. Only that part of a chemoreceptor cell initially acted upon by chemical stimuli from the animal's environment will be referred to as the "receptor site." The physiological events at the receptor site will be designated as the "initial excitatory mechanisms." The total process of "excitation" of the chemoreceptor cell could also include any other physiological processes (in addition to the initial excitatory mechanisms) which lead to the rapid depolarization of the cell membrane always associated with the "spike potential" of the nerve impulse. The tenuous grounds for classification of insect sense organs as "olfactory" or "gustatory" have been discussed in detail by Dethier & Chadwick (2) and Hodgson (11), and these terms will be employed here as a matter of convenience, rather than to perpetuate the probably erroneous view that olfaction and gustation involve distinctly different physiological mechanisms.

THE CHEMORECEPTOR CELL

Arthropods Other than Insects

Barber (12, 13) has recently described some of the functional properties of chemoreceptors in the earliest phylogenetic type of arthropod now accessible for experimentation, the horseshoe crab, *Limulus polyphemus* Linnaeus. The chemoreceptor cells are located in spines on the gnathobase, a medial

projection of the walking leg coxal segment. The receptor sites appear to be at the integumentary surfaces of cuticular tubules on the gnathobase spines. A cuticular canal connects the tubule with a group of sensory cells in the spine lumen, although it is not known (14) whether there is a one to one relationship between the receptor sites and the cell bodies of the sensory cells underlying the spines. The distal process of the chemosensory cells appears to be always smaller in diameter than the diameters of proprioceptor nerve fibers. By lifting bundles of nerve fibers teased from the gnathobase nerves onto silver electrodes connected to an amplifier and cathode-ray oscilloscope. it was possible to monitor and photographically record the afferent nerve impulses passing along the nerve fibers. [The theory of electrophysiological recordings of nerve impulses has been described with particular reference to insects by Roeder (15)]. Flooding the ends of the gnathobase spines with extracts of the soft parts of clams (*Venus* and *Mya*) evoked massive, long-lasting barrages of action potentials in the gnathobase nerve fibers. The stimulating component of the extracts was found to be heat stable, dialyzable, and to form colorless aqueous solutions. The same solutions which stimulate the chemoreceptor cells also initiate feeding behavior in the intact animals.

The afferent impulses from chemoreceptors and thermal or tactile rereceptors can be differentiated in a number of ways. Strong acid applied to the surface of the gnathobase spines renders the chemoreceptor cells refractory to further chemical stimulation, but the thermal and tactile receptor cells are apparently unaffected. Tactile responses consist of larger voltage spike potentials and are more rapidly adapting than responses from chemoreceptor cells. Thermal receptor cells appear to share many properties with tactile receptors, and there is a possibility that some of the same receptor cells may be responding to both types of stimuli. When the gnathobase spines were bathed in sea water alone, without the addition of chemicals, "spontaneous" activity of chemoreceptors could be recorded.

Barber's description of the chemoreceptors of *Limulus* makes it clear that many of the basic properties of chemoreceptor cells in arthropods were established at an early stage in the evolution of the phylum. These properties would include: relatively small diameter fibers (resulting in relatively small amplitude spike potentials), relatively long adaptation periods during constant stimulation, and some low-frequency spontaneous activity. The latter activity is "spontaneous" of course only in the sense that it occurs in the absence of added chemical stimuli of the usual sorts. Other chemosensory organs, sensitive to dissolved gases, are thought to be present on the general body surface of *Limulus* (16), but their structure and exact functions are unknown. Chemosensory organs about which precise physiological data are lacking have been described for many crustaceans. Doflein (17) reported that the small antennae were used in responding to chemicals by various decapods. Luther (18) found chemosensory organs on the mouth-parts, walking legs, and pincers of brachyurans. The physiological analysis of the functions of

chemoreceptor cells in those various locations awaits further adaptations of the electrophysiological techniques.

By recording the electrical components of chemoreceptor cell activity, using fluid-filled electrodes external to the cuticle, Hodgson (19) found that single chemoreceptor cell preparations could be studied on the legs of the crayfish *Cambarus bartonii sciotensis* Rhoades. The chemosensory organs are tufts of setae arising from depressions in the cuticle on the chelae and protopodites of the first two pairs of walking legs. During tests with a series of sugars, salts, and other chemicals in pure form, it was found that the chemoreceptor cells on the walking legs of *C. bartonii sciotensis* were activated only by amino acids, of the test series used. Only the amino acids initiated feeding reactions of intact crayfish, so that a good correlation between chemoreceptor cell activity and behavior exists in this case, as with *Limulus*.

The physiology of chemoreceptors in arachnids has not been studied, and very little information exists which would indicate where to find them. McIndoo (20) concluded that the lyriform organs on the legs of spiders are olfactory organs. Bipolar neurons have been described in the lyriform organs, but contradictory observations were recorded concerning the manner in which the distal processes of these cells terminate, and their true function remains to be determined. Similar sense organs occur among the phalangids and pseudoscorpions. Recent behavioral data indicate that well-developed chemical senses exist in ticks (21) and mites (22). In a very exhaustive study, Camin (22) narrowed down the chemoreceptor area to clumps of sensory setae on the tips of the tarsi in the snake mite, *Ophionyssus natricus* Gervais, and reported that the receptor cells apparently respond to oils secreted by the epidermal glands of living snakes. The small size of the mites makes it unlikely that physiological studies could carry the analysis further in the near future.

Cloudsley-Thompson (23) has recently described the sensory physiology of the Diplopoda. In one species of millipede, *Pseudopolydesmus serratus* Say, afferent impulses from chemoreceptor cells have been recorded electrophysiologically by Hodgson (19). The receptor cells appear to lie within small trichoid sensilla on the tarsi and to respond to sugars. Attempts to record receptor cell activity from the antennae were negative, although the small size of the receptor cells may account for this. Behavioral tests have shown that millipedes feed readily upon sugars placed in contact with the tarsi, even after the antennae have been removed, thus corroborating the electrophysiological results (19).

Insects

More information exists concerning the chemoreceptor cells of insects than for any other group in the animal kingdom. It is generally agreed that the chemoreceptor cells of insects are modified epithelial cells and that the central axon is formed by the ingrowth of processes from these cells to the central nervous system—i.e. that the receptor cells are true "primary sense

cells" (24). Certain anomalous cases, in which the presumed chemoreceptor cells do synapse with other neurons just under the sense organs, have recently been described by Eisner (25), however. In regard to the old problem of what happens to the receptor cells when the bulk of the sense organ is shed at moulting, there have been two views. It has been reported that the receptor cell detaches from the old sensillum before moulting and is later re-encased by a new sensillum, or, that the distal tip of the receptor cell process is broken and regenerated (26). Actually both mechanisms have been shown to operate, even in the same insect (27). Thus, the behavior of the chemoreceptor cells during moulting supports the histological evidence that the peripheral sensory cell itself, rather than any outgrowth from a cell body within the central nervous system, generally, produces the outgrowths both to the tip of the sense organ and to the central nervous system.

The fact that many chemoreceptor cells of insects are known to be primary sense cells results in an exceptionally favorable condition for their physiological study. Nerve impulses recorded from central axons of such single chemoreceptor cells can be reasonably assumed to represent the afferent nerve "messages" from single receptor cell units, unaltered by any changes which might occur at synapses. Such a condition exists in most known gustatory chemoreceptor cells of insects. Olfactory chemoreceptor cells are also commonly regarded as primary sense cells, but the proximal filaments from many olfactory receptor cells may fuse to form a single compound axon, and if this were not so, it is obvious that a structure such as the antenna, which may contain many thousands of receptor cells, would have to be much larger than its actual size (24). For this reason, and because of difficulties in exact quantitative controls during administration of gaseous stimuli, the physiological analysis of olfactory receptors is considerably more difficult than for gustatory receptors, and the two general types will be discussed separately here.

Gustation.—The experimental material which has proved to be the most productive in recent years, with regard to studies on insect gustation (or "contact chemoreception"), consists of tarsal and labellar chemoreceptors of the blowfly, *Phormia regina* Meigen. The first single chemoreceptor cells of *Phormia* to be studied in detail were those underlying setae on the tarsus, as localized independently by Lewis (28) and by Grabowski & Dethier (29). The latter authors removed flies from puparia one or two days prior to their emergence dates and vitally stained the receptor cells by immersing the flies in methylene blue. In order to section the cuticle of the flies without disrupting the normal relationships of the cuticle to the underlying hypodermis, a methacrylate embedding medium was used. This made possible the cutting of one and two micron sections with an ordinary microtome. The maximum number of receptor cells innervating a single tarsa hair of *P. regina* was found to be three, but some hairs appeared to lack innervation, and sometimes only one or two sense cells were found associated with each hair. Lewis (28) reported six to eight receptor cells associated with a single sensillum on the

tarsus of *Phormia terraenovae* R.-Desvoidy. When, in *P. regina*, three receptor cells were found underlying a single sensillum, only two of the cells sent processes to the tip of the hair, which enclosed the actual receptor site, as shown by behavioral tests.

Chemoreceptor cells with much lower thresholds and more accessible for experimentation, have recently been described by Dethier (30). Three bipolar neurons are associated with each hair on the labellum of *Phormia*, but only two of the receptor cells send processes to the tip of each hair. Both of these cell processes pass through a small cavity inside the hair, and both processes terminate at a papilla on the tip of the hair. The histology of the labellar chemoreceptor cells and associated structures has also been studied by electron microscopy (31). The following are measurements of the chemoreceptor cell dimensions in fixed material: cell body diameter, 7 to 9 μ; proximal fiber, 0.5 to 1 μ diameter; distal fiber (near tip of hair), 0.1 μ diameter. Where comparisons of living and fixed materials are possible, it appears that fixation may result in shrinkage of the cell processes to approximately one-half of their size in the living state. The anatomy of the labellar hair is shown diagrammatically in drawing *A* of Figure 1. Smaller chemosensory structures also occur on the labellum of *Phormia* and have been designated the interpseudotracheal papillae. Two neurons (possibly a third neuron also) innervate each papilla. The sizes of these receptor cells are approximately the same as those associated with the longer hairs on the labellum.

By rolling a droplet of sucrose solution along the shaft of a labellar hair, Dethier showed that the fly does not give a behavioral reaction (proboscis extension) until the droplet reaches the tip of the hair. The initial excitatory site must be located at the papilla. The behavioral effects of 75 different carbohydrates applied to the tips of single labellar hairs have been noted, and it appears that any one labellar hair is sensitive to the same compounds as any other labellar hair, or, in other words, that there are not specific hairs for specific sugars.

The labellar chemoreceptor cells of *Phormia* were the first primary chemoreceptor cells to be directly studied electrophysiologically. While the receptor cell processes are too small to be amenable to any of the usual electrophysiological techniques, this difficulty was circumvented by recording the action potentials of the receptor cells through the same solution used to stimulate the cells. The procedure, as reported by Hodgson *et al.* (9), is diagrammed in Figure 1 *A*. A pipette containing the stimulating solution is connected via a silver-silver chloride electrode and cathode follower to an amplifier and cathode-ray oscilloscope. At the instant the solution within the pipette makes contact with the tip of a labellar hair, a stimulus artifact, followed by spike potentials from the chemoreceptor cells, is registered as a series of deflections of the beam of the oscilloscope. Essentially, this method makes it possible to visualize and photograph the afferent impulses which

constitute the information passing to the central nervous system from the chemoreceptor cell. Operative trauma to the preparation is minimal, and preparations may be stable for several hours. In actual practice, it is convenient to record the spike potentials on a tape recorder, permitting later replay for inspection or photographing (see Figure 1).

The electrophysiological studies have revealed several properties of chemoreceptor cells which have not been accessible to investigation by any other technique. By an appropriate arrangement of electrodes, it is possible to distinguish the spike potentials coming from each of the two chemoreceptor cells innervating a single labellar hair. Smaller amplitude impulses (designated *S* spikes, from the *S* receptor) are evoked only when the hair is being stimulated with sugars, while larger amplitude impulses (designated *L* spikes, from the *L* receptor cell) are evoked by various nonsugars, including salts, acids, and alcohols (9). Record *C* of Figure 1 is taken from a labellar hair being stimulated with 0.5 *M* NaCl; the response consists entirely of *L* spikes. Record *D* of Figure 1 is taken from the same labellar hair during stimulation with 0.25 *M* sucrose mixed in 0.1 *M* NaCl; the record shows a predominence of *S* spikes with this mixture. In the intact fly stimulation of the *L* receptor cell leads to absence of a feeding reaction, or to a rejection response, while stimulation of the *S* receptor cell leads to proboscis extension, a part of the normal feeding behavior. This relationship will be discussed in more detail below.

Perhaps the most surprising feature of both *S* and *L* receptor cells is the fact that, in apparent contradiction to the law of specific nerve energies, they also respond when the temperature of the preparation is changed or when the labellar hair is bent. The magnitudes of these thermal and tactile stimuli are well within normal physiological ranges (32). The initial excitatory sites within the receptor cell, however, do not appear to be identical with the different types of stimuli. While chemicals normally affect the tips of the distal cell processes, the temperature effects are localized at or proximal to the cell bodies of these receptor cells (33). A similar localization of the sensitivites to temperature and tactile stimuli is suggested by the fact that responses to mechanical movements may be obtained for a short time even after the distal half of a labellar hair is removed. The sensitivity of chemoreceptor cells to other modalities of stimuli within normal physiological ranges has been observed in the labellar and tarsal chemoreceptors of other flies and in the tarsal chemoreceptors of various butterflies (19). These observations illustrate the impossibility of determining the function of a particular cell or sense organ by using anatomical or behavioral observations alone.

The possibility that a single receptor cell may have several initial sites of excitation, depending upon the type of stimulus, raises the question of what localized specializations of the cell's structure and function account for such sensory versatility. Data indirectly pertinent to this problem have been presented by Roys (34), who compared the sensitivites of taste receptors and of

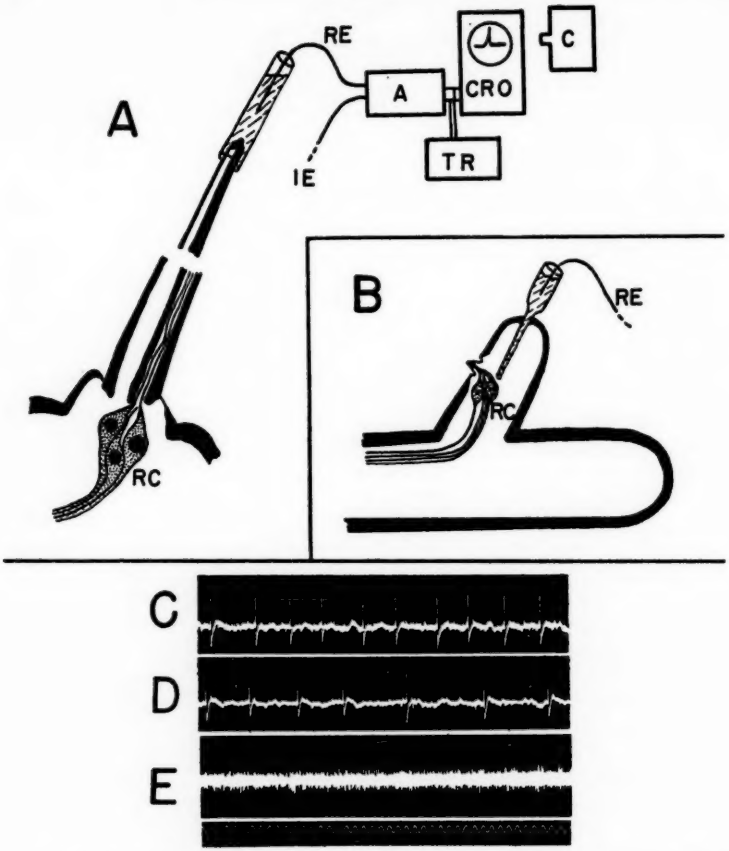

FIG. 1 *A*—recording set-up with labellar hair of *Phormia* and external fluid-filled electrode; *B*—use of capillary microelectrode to record from olfactory cells in antenna of *Bombyx*, (redrawn after Schneider); *C*— *L* fiber response from labellar hair of *Phormia* during stimulation with 0.5 molar NaCl; *D*— *S* and *L* fiber response from same hair as record *C*, but during stimulation with 0.25 molar sucrose mixed in 0.1 molar NaCl; *E*—spontaneous activity from many olfactory cells in the antenna of *Amoebaleria*, as recorded with external fluid-filled electrode. Time base for all records, 100 c.p.s. The following abbreviations apply to all records: RC, receptor cells; RE, recording electrode; IE, indifferent electrode; A, amplifier; CRO, cathode-ray oscilloscope; TR, tape recorder; C, camera. Additional explanatory notes in text.

nongustatory nerve tissue of the cockroach, *Periplaneta*. It was found that nerve fibers and neurons in the tarsi and ventral nerve cord responded to direct application of salt, acid, sucrose, and quinine in concentrations as low or lower than the concentrations which have been reported as normal taste thresholds in behavioral studies. This suggests that great sensitivity to the chemical environment is simply a basic property of many neurons, and that certain neurons function as chemoreceptors simply because they are located in positions exposed to chemicals, and not because of any particular specialization for being excited by the chemicals. While this theory may be true in some cases, the demonstrated range of chemical sensitivities of the *S* and *L* labellar receptors (32) argues against a universal application of this view.

Olfaction.—Since the review of olfaction by Dethier (35), the principal contribution to the study of olfactory receptor cells of insects has been through the electrophysiological analysis of Schneider & Hecker (36). By introducing glass capillary microelectrodes into the antenna of the male silkmoth, *Bombyx mori* (Linnaeus), these workers were able to approach the cell bodies of a few olfactory chemoreceptor cells and to record spike potentials associated with their activities. Spontaneous impulses were recorded in the absence of any applied stimulus, and the frequency of impulses increased during exposure of the antennae to vapors of cycloheptanon, sorbinol, or the sexual attracting substance of the female moth, as partially isolated in extraction procedures carried out by Butenandt (37). The antennae of female moths give responses to sorbinol and cycloheptanon but not to the sexual-attracting substance. Vapors of ether or chloroform were found to suppress the spikes. The recording setup used in these studies is diagrammed in drawing *B* of Figure 1.

By using D-C amplification of the slow electrical potential differences between the tip and the base of an amputated antennae, Schneider (38) has also obtained an "electroantennogram," or EAG. The form of the EAG depends upon the odor applied, but all records show an initial increase in negativity at the tip of the antenna. The results suggest that the slow potentials are summations of electrical changes in many receptor cells, for certain consistent relationships to the results recorded through capillary electrodes are apparent. Unfortunately, the close spacing of receptors on the antennae of most insects makes it difficult to apply the technique of fluid-filled electrodes external to the cuticle. In the helomyzid fly, *Amoebaleria defessa* Osten-Saken, however, it is possible to record the activity of the antennal receptor cells from the enlarged third segment of the antenna using the external electrode technique (19). A typical record is shown in photograph *E* of Figure 1. The variety of spike heights indicates that many cells are contributing to the record, and the smaller sizes of the spikes, relative to the base-line "noise" from the apparatus, indicates that these receptors are probably smaller than the labellar receptor cells from which records *C* and *D* were taken.

Roys (39) has shown that burst of spike potentials in the antenna of the cockroach *Periplaneta americana* (Linnaeus), which are too low in amplitude to be recorded as individual spikes, can be recorded as slow over-all potential changes. His studies, however, dealt with chemicals believed to have general effects upon nerve tissue—examples of the so-called "common chemical sense"—rather than normal olfactory stimulants, and the relationship between such results and chemoreception is unknown. Certainly the antennal recordings made from cell bodies of the olfactory receptors, and by summing the electrical changes in populations of olfactory receptors seem to offer a way of analyzing many problems, including the basis for species specificity of sexual attractants, relative stimulating effectiveness of attractants and repellents, etc.

MECHANISMS OF EXCITATION

Clues to the mechanisms of excitation of chemoreceptor cells have been sought by trying to determine what characteristics of chemicals are responsible for their stimulating effectiveness. The most extensive work comprises the experiments of Dethier & Chadwick on *Phormia regina*. The tarsal chemoreceptors are exposed to varying concentrations of chemicals in solution, and thresholds are determined on the basis of the subsequent behavior of the flies, with proboscis extension the criterion of stimulation of the receptors. Much of the work has been so recently reviewed (7, 8) that only the general principles emerging will be discussed here.

The most important characteristics of stimuli differ according to the type of compound being tested. In the case of organic compounds, the closest approach to a unifying principle is the correlation between lipoid solubility and stimulating capacity (40), although exceptions must be made in the case of certain compounds (2). This concept can be used to explain such data as the increase in stimulating effectiveness of organic compounds with increasing chain-length of the molecules, and the increased stimulating capacity of those chemicals having functional groups which decrease the water solubility.

The most specific action upon chemoreceptor cells is exhibited by the sugars. In a large series of tests performed on both populations of tarsal receptors and upon single labellar hairs of *Phormia*, Dethier found that, as had been previously been recognized by von Frisch (41) and by Hassett *et al.* (42), possession of an alpha-D-glucopyranoside link in the molecule is the most important characteristic determining the stimulating capacity of a sugar. For example, maltose with a 1, 4 linkage, turanose with its 1, 3 linkage, and the non-reducing sucrose are stimulating sugars, whereas lactose with its 1, 4 linkage and melibiose with its 1, 6 linkage both lack the alpha link and are non-stimulating. The effect is never all or none, but invariably the compounds with the alpha link are superior stimuli. As an example of the differences between stereoisomers, it was reported that D-arabinose is markedly more stimulating than L-arabinose (30).

The specificity of the sugar effects, and the mutually exclusive sensitivities of sugar and non-sugar receptor cells as studied electrophysiologically, suggests that there is a highly selective receptor substance or site with which the sugar must react. Whatever process occurs at the initial excitatory site must also be independent of temperature changes. Frings & Cox (43) have observed small effects of temperature in changing thresholds of flies, and temperature effects upon the cell bodies of the receptor cells are known (32), but none of these cases demonstrate temperature effects at the initial excitatory site. Stimulation by sugars is not blocked by phlorizin, fluoride, azide, iodoacetate, or cyanide, and must not involve any steps in the glycolytic cycle below those blocked by the agents listed (8). The simplest hypothesis of a mechanism of sugar stimulation in accord with these facts seems to be that the sugar molecule combines reversibly with a receptor substance to form a complex at the initial excitatory site. The combination probably involves weak forces such as Van der Waal's, and it is envisioned that the complex depolarizes the cell membrane, after which it is removed passively by a shift in concentration gradient. The merits of this and several more elaborate alternative hypotheses have been discussed by Dethier (8).

The stimulating capacity of electrolytes has been identified primarily as a function of the cations (44, 45). By testing various cations in uniform anion combination it has been possible to demonstrate that the relative effectiveness of the cations parallels the order of ionic mobilities. Exceptions to this rule occur among the divalent salts, however. The order of effectiveness of various anions in uniform cation combination has not been satisfactorily explained. The outstanding theory of a mechanism for stimulation by electrolytes is that of Beidler (46), based upon studies of mammalian chemoreceptors, but probably applicable to the chemoreceptors of insects as well. Beidler postulates that cations are bound to natural polyelectrolytes such as nucleic acids at the receptor surface, resulting in depolarization of the receptor cell membrane. This theory is in accord with the temperature independence of the initial excitatory mechanisms, the known speed of stimulation, and other features of the process, but it has not yet been subjected to all the tests which would be appropriate with insect chemoreceptors.

It is not yet clear whether the initial depolarization of the receptor cell membrane is the same depolarization which produces the spike potential of the nerve impulse. The initial depolarization may possibly be a slower wave of depolarization which spreads along the distal process of the cell to the cell body, where the actual spike potential might be produced. Hodgkin & Rushton (47) have discussed the conditions under which electrotonic spread may be effective in propagating excitation, and, using their data, Dethier (48) has calculated the space constant for electrotonic spread of depolarization in the distal processes of the labellar chemoreceptor cells of *Phormia*. The results indicate that the hypothesis of electrotonic spread from the initial excitatory site to the cell body is theoretically possible, and such a process may be involved in the explanation of why temperature appears to affect one part of

the chemoreceptor cell and not another, why impulses can be obtained in response to bending a labellar hair even after the tip of the hair is removed, etc.

Drug and insecticide actions.—Very few drugs or insecticides have yet been tested under conditions which have permitted conclusions concerning their effects specifically upon chemosensory organs. Smyth & Roys (49) found that low concentrations of DDT, while apparently not stimulating by themselves, did unstabilize chemoreceptor cells so that trains of afferent impulses, rather than the normal frequencies of impulses, are generated in the receptor cells. Previous treatment with DDT lowers, about ninefold, the sucrose acceptance thresholds of DDT-sensitive houseflies and blowflies, while sucrose thresholds of resistant flies are unaltered. Hodgson & Smyth (50) took advantage of the sensitivity of chemoreceptor cells to DDT in developing a method for identifying chemoreceptor impulses in recordings made from large populations of nerve fibers. Many inhibitors of steps in the glycolytic cycle have been tested upon the *S* receptors of *Phormia* and have had no apparent effects (8). Acetylcholine, postulated to play an important role in certain chemosensory systems of mammals, is also without apparent effects upon the labellar receptors of *Phormia* (4). This is obviously an area which offers many promising experimental possibilities for future study of insect attractants, repellents, and drugs with highly specific effects upon intermediary metabolism.

THE SENSE ORGAN

The influence of other parts of the sense organs upon the chemoreceptor cells has recently been investigated with particular regard to the cuticle, as it may influence the types of chemicals gaining access to the initial excitatory site, and there has also been concern with possible interactions between adjacent chemoreceptor cells. All evidence suggests that the cuticle overlying the distal tip of the sense organ has special permeability characteristics. The existence of hydroreceptors (4), despite the generally hydrophobic properties of the epicuticle, is one indication of this. The nature of the cuticular specializations was investigated by Richards (51), who found that the thickness and the degree of sclerotization of cuticle overlying the sense plates on the antenna of the honey bee differed from the thickness and sclerotization of cuticle adjacent to these receptors. Slifer (52) was able to demonstrate the passage of aqueous solutions of dyes, such as acid fuchsin, through the tips of large basiconic sensilla on the antennae of grasshoppers. It appeared that the entire outer surface of these sensory pegs must be waterproof except at the distal tip, where the usual waxy or lipoid layers of cuticle were found to be missing. This interpretation correlated with Dethier's finding that a droplet of sucrose rolled along the length of a labellar hair of *Phormia* stimulates only at the tip of the hair (30); and the fact that electrical resistance at the tip of a labellar hair is less than at any other part (9). Slifer also subsequently demonstrated that the smaller sensilla basiconica on the grasshopper antenna

have water-permeable spots, not at their tips, but near their bases (53). Additional study of the fine structure of the long antennal sensilla basiconica led Slifer, Prestage & Beams (27) to conclude that no cuticular covering of any sort is present over the distal tips of these hairs. This is the first demonstration with any species of insect that the tips of the distal processes of olfactory chemoreceptor cells are freely exposed to air. To explain how the nerve endings are kept moist it is postulated that the vacuole of the trichogen cell, which passes up the lumen of the sense organ, may act as a reserve supply of fluid which counteracts the very slow loss of water from the tip of the sense organ. It appears then that the initial excitatory sites of some chemoreceptor cells have direct access to the atmosphere, while differential permeability of overlying cuticle explains the contact of other chemoreceptor cells with chemicals in the environment.

The postulated role of the trichogen cell in moistening the receptor cell ending is only one of several possible cases of mutual relationships between the cells associated with any one sense organ. The function of the third neuron underlying each labellar hair of *Phormia* is, for example, completely unknown at present (32). It has been noted that when the *L* receptor is active in *Phormia* that the *S* receptors tend to show decreased freuqencies of afferent impulses. Although the mechanism producing this effect is unknown, it undoubtedly has considerable significance for understanding the behavior of intact flies, since it would tend to increase the contrast between acceptable and unacceptable stimuli (54). Photoreceptors in *Limulus* eyes exhibit mutual inhibitions of this type which enhance visual contrast (55), but the mechanism of the interaction is unknown in this case also.

PERIPHERAL AND CENTRAL NERVOUS INTEGRATION; BEHAVIOR MECHANISMS

The results of most recent experiments support the view that the behavior of insects can be predicted to a large extent from an accurate knowledge of the functions of peripheral receptor cells. Since *Phormia* gives a positive feeding reaction (proboscis extension) only in reaction to stimulation by sugars, a peripheral discrimination mechanism for acceptable and unacceptable stimuli is indicated in this most thoroughly studied case. Thus, if the *S* receptor is stimulated, the fly gives a feeding response, while if the *L* receptor is stimulated, the fly gives a rejection response. In a more extensive survey of the effects of 23 carbohydrates upon the labellar chemoreceptor cells, Hodgson (54) extended the evidence for the very exact relationship between behavior and activity of primary chemoreceptor cells, showing that absence of a feeding response may be caused by failure of a chemical to stimulate the *S* receptor, by strong stimulation of the *L* receptor, or by inhibition of both *L* and *S* receptors. Thus, the distinction between "repellent" and "inhibitory" compounds also appears to have some basis in terms of the effects of the two categories of compounds upon the labellar chemoreceptors of

the blowfly. Electrophysiological analysis of chemoreceptor cell activity can thus detect some of the different mechanisms underlying behavior more precisely than can behavioral analysis alone. This suggests the possibility that reactions to food materials, attractants, repellents, or poisons might be predicted by convenient laboratory analysis of receptor cell activities rather than by behavioral and field studies exclusively.

Afferent impulses from chemoreceptors in different parts of the body are summed in the central nervous system, as shown by the fact that thresholds for sucrose stimulation are lower when two legs of *Phormia* are exposed to the sugar than when unilateral stimulation is applied. Unacceptable compounds also "sum" contralaterally, and the prevention of a feeding response to water and sucrose by unacceptable compounds is predominently a phenomenon of the central nervous system (56). Adaptation during constant stimulation occurs in both the peripheral and central nervous systems (32, 57), and the termination of feeding appears to be influenced, but not entirely explained, by such adaptation (58).

Dethier, Evans & Rhoades (58) have constructed a picture of the delicate balance of mechanisms controlling the feeding reaction of the blowfly. Normally the antennal or tarsal chemoreceptors initiate the reaction, but chemoreceptors on the mouthparts ultimately exert a tighter more delicate control over what is ingested. During actual feeding, interpseudotracheal papillae on the lobes of the labellum supply the main chemosensory stimulation, and it would be interesting to know if the chemoreceptor cells in these papillae exhibit relatively little or slow adaptation rates, as might be expected. Curiously, neither gut capacity nor carbohydrate requirements appear to control the volume of food ingested (58, 59), nor is there any good correlation between nutritive value of carbohydrates and thresholds of response to them (42). In the lack of an apparent tendency for constant intake of food, the insects differ markedly from mammals, and pose many problems yet to be solved (4).

Schwinck (60, 61) has recently provided an analysis of a complex reaction to olfactory stimuli. She studied the mechanism of attraction of male silkmoths, *Bombyx mori* (Linnaeus), to the female silkmoths, Contrary to early assumptions, it appears that the female scent merely "releases" an automatic "searching" behavior of the males. Summation of activity from several antennal receptors or else extremely strong stimulation of a few chemoreceptors is necessary to reach a central nervous system threshold for releasing the male's activity. The males appear to orient against the wind, and only later orient specifically to the scent of the females. These results seem to imply involvement of tactile or visual receptors in the initial flight reactions of the males, but the origin and exact role of such additional sensory cues is yet to be explained. Progress with purification of the sex attractant discharged by the female of *B. mori* has been reported by Butenandt (37), Hecker (62), and by Makino *et al.* (63). Wharton, Miller & Wharton (64)

have described a bioassay used as an adjunct to the chemical analysis of an odorous substance found on virgin female cockroaches, which attracts male roaches. Unfortunately, space does not permit the description of many valuable studies of behavioral mechanisms involving chemoreception, but the recent studies of Camin (22), Edwards (65), and Schaeffenberg & Kupka (66) are especially noteworthy.

ECOLOGICAL AND EVOLUTIONARY SIGNIFICANCE

Historically, the ecological aspects of chemoreception in insects were the first to receive attention. The classic instances, involving the role of odors in mating behavior and food plant selection, are too well known to be discussed again here (2, 3, 4, 5). As behavioral studies have attained new levels of sophistication, however, it appears that many reactions mediated by chemoreceptors have a very different significance from the seemingly most obvious one. Thomas (67), for example, has shown that food preferences of the fly *Sarcophaga*, while apparently playing no part in the actual selection of individuals of the opposite sex, are important in bringing the sexes together in the same localities. A more specific type of chemical stimulus causing aggregations of the housefly *Musca* has been demonstrated by Barnhart & Chadwick (68). Houseflies visiting a bait contribute to it some substance ("fly-factor") which enhances the attractiveness of the bait to other flies. The most detailed analysis of the role of chemoreception in reproductive behavior has been made with the fruit fly, *Drosophila*. Mayr (69) showed that sexual isolation between different species almost completely disappears under optimal experimental conditions if the antennae of the females are removed. Spieth (70) has concluded that psychological isolation of this type characteristically precedes any morphological differences in the evolution of species.

Most of the instances of chemoreception of greatest importance in ecology and evolution involve very specific or selective responses to "token" chemical stimuli (71), and accounting for the specificity of the insect's response remains a problem of widespread significance. The electrophysiological studies of Schneider (38) demonstrate that a narrow range of sensitivity in the chemoreceptor cells may account for some of the cases, but much more undoubtedly might be done in the near future to differentiate selective sensitivity of chemoreceptor cells from central nervous and other mechanisms leading to highly selective and stereotyped responses.

The most outstanding incidence of presumed central nervous mechanisms underlying specificity in responses to chemicals is the well known phenomenon of olfactory conditioning, described by Thorpe & Jones (72). Is this "conditioning" really a change in some central nervous integration mechanisms as the same might suggest, or are there other physiological alterations of the animals so affected? Le Magnen (73), following up clinical observations on olfactory sensitivity in humans, found that thresholds to certain substances were lowered by injection of the chemical into the patients. The

effect lasted as long as thirty days and resembled a process of immunologic sensitization. Le Magnen postulates that a similar process may underlie the species specificity of olfactory responses and the discrimination of a particular host by a parasite (74). The possibility of a parallel between the action of ingested materials causing olfactory conditioning and of injected materials causing an immunologic reaction has not been explored, and might be expected to provide a valuable lead into this little understood process which appears to be of general significance in assisting the invasion of new habitats by conspecific populations (75).

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INTERNAL SYMBIOSIS IN INSECTS[1,2]

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Anyone acquainted with the monumental monograph by Buchner (11) knows that a voluminous literature exists dealing with the microorganisms symbiotic or supposedly symbiotic in insects. In recent years an international symposium and numerous review articles, particularly in Europe, have been published (10, 16, 18, 23, 29, 35, 37, 40 to 47, 49, 73, 74, 77 to 80, 83). With so many recent treatments, one may well ask why another is being published. In accepting the invitation to write on this subject we had in mind both the value of different points of view and the possibility of preparing a treatment which will be partly a review of work published subsequent to Buchner's monograph and partly an essay on what seems to us the current status, limitations, and pitfalls of work in this fascinating branch of ecology (or physiological ecology).

The field of ecology may be subdivided in various ways. One way is to divide the material into two sets, one dealing with the reciprocal effects between organisms and the inanimate world, the other with the reciprocal effects of organisms on one another. Intimate association of two organisms is termed symbiosis. It becomes most intimate when one organism lives inside the other. Such associations may be further subdivided (see any standard work in ecology). If neither profits in an obvious manner the association is called commensalism and the members commensals; if one member only is thought to profit the association is called parasitism and the members are called host and parasite; if both members are known or thought to profit the association is called mutualism and the members are called host and symbiote. There is some disagreement in the literature on the use of the words symbiosis and symbiote [commonly spelled symbiont, see Steinhaus (74)]. It is not our purpose here to harangue on terminology; suffice it to say that we will use "symbiote" for the microorganism and "host" for the larger organism (insect) involved in a mutualistic or seemingly mutualistic association.

From the ecological point of view, the host is the environment of the symbiote (the host is also the environment for an internal parasite). But since the environment is a living organism, further analysis quickly becomes

[1] The survey of the literature pertaining to this review was completed in May, 1957.

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physiological even though we are dealing with an ecological association. With slight modifications, the equipment and techniques are those used in physiological and microbiological laboratories, and little is to be gained by further belaboring the ecological nature of the association.

Although the analysis of these associations requires physiological methods, most of the available information comes from deductions based on comparative descriptive studies. This type of approach has been called "letting nature perform your experiments." It is the basis of comparative anatomy and of most studies in phylogeny. It is a powerful tool in many other fields. Certain aspects of chromosome cytology, of the mechanism of mitosis and meiosis, of embryonic processes, etc., have derived much from the comparative approach. Or, to use another sort of example, examination of the chapter on reproduction in Wigglesworth's well-known textbook will show that little can be written on insect reproduction today except for data of this sort. The comparative approach is a powerful one, and Buchner (16) feels it should be continued exhaustively, but many of the questions raised require laboratory experiments.

Over and over again we encounter a situation in which we could speculate better about symbiotic phenomena if we knew more about the precise causes of general biological phenomena: the precise nature of penetration of large bodies such as sperm and bacteria through membranes, the real nature of sex determination, of cellular tropisms *in vivo*, of natural in contrast to acquired immunity, etc. Many of the problems we are trying to explain are concerned with special cases of general phenomena that have so far defied analysis.

Here a few more definitions are required for clarification. An insect species which harbors beneficial microorganisms is called a symbiotic species; others which do not are called asymbiotic. Since it is sometimes desirable to distinguish between species which regularly lack symbiotes and ones from which the normal symbiotes have been eliminated, the latter may be called aposymbiotic. In a few cases hierarchies of symbiosis are known or suspected. Thus, Schmidt (71) and some previous authors have suggested that the flagellated protozoa living symbiotically in the intestine of termites have intracellular bacterial symbiotes. (Numerous hierarchies are known in parasitology; most comparable being cases such as the intestinal amoebae of mammals which cannot persist in an intestine freed of bacteria). When the symbiote is inside its host, it may be called endosymbiotic; if inside cells, it may be classed as intracellular. If the insect differentiates a special organ for harboring the symbiotes, this is called a mycetome. If visibly distinct cells are differentiated for holding the symbiotes, these are called mycetocytes (bacteriocytes). Mycetocytes may be grouped together to form a mycetome or may be scattered throughout the body.

The present review deals only with internal symbiotes. In some cases these are extracellular, in some cases intracellular. Usually the location of the supposed microorganism is perfectly clear but sometimes it is difficult to

place precisely. For example, when Wigglesworth first worked on *Nocardia* in the gut of *Rhodnius* he described it as both in the lumen and in the gut cells. Closer study led to the conclusion that it is always extracellular or intercellular (83). Internal symbiotes may be found in the gut lumen, between gut cells, in gut cells, in lumen of a mycetome that is a diverticulum of the gut, in mycetocytes which are aggregated into a mycetome or separated and scattered (usually in the fat body), in the ovarioles and later in eggs and embryos, and, in other cases free in the hemolymph (75). In general, those found in the gut are transmitted to the next generation as contaminants on the egg or associated with larval feeding, whereas those in mycetocytes are transmitted transovarially inside the egg [see Buchner (11)]. The latter method is sometimes referred to as "transovarial infection" or "hereditary transmission."

The Origin of Symbiotic Associations

The wide scattering of symbiotes among diverse groups of insects is interpreted as meaning that symbiosis has arisen many times during the course of insect evolution. Only in the cockroaches do we have the situation where all examined species of a whole order contain similar-appearing "bacteroids" which are housed and inherited in a similar manner.

In many cases sensible correlations can be made between the type of food eaten and the presence or absence of symbiotes. Thus, blood-sucking species, wood-borers, stored-grain pests, and plant-sap suckers usually harbor microorganisms. This is commonly interpreted as indicating that the symbiotes permit utilization of foods and habitats not otherwise nutritionally adequate. But imperfections in the correlation show both that other means exist for attaining this end and that symbiotes perform other functions. Thus, some wood-boring beetles appear to be devoid of symbiotes (44), and in certain cases other functions such as sex determination (13) and mobilization of urates (79) appear to be served. Commonly it is assumed that if an associated microorganism is not clearly parasitic or pathogenic, then it must be mutualistic (e.g., 59). If this attitude is taken, it follows that the associations are not always necessary. For example, strains of *Sitophilus granarius* (Linnaeus) are known with and without symbiotes; they differ only in seemingly trivial details of color and size as first pointed out by Mansour many years ago (55, 72). Another beetle, *Rhyzopertha dominica* (Fabricius), is reported by Huger (36) as showing no effect at all from removal of its symbiotes. This disturbs Huger who seems to feel that an insect would hardly develop so specialized a structure as a mycetome unless it were needed. Personally, we see no reason why an association cannot be beneficial without being necessary (one could draw a parallel to the utilization of metabolic water, a power that is seldom "necessary" even for those few species which can do it sufficiently).

A current vogue in the Buchner-Koch school is to argue that mutualism is evolutionarily distinct from parasitism and cannot arise from rendering a

parasite harmless. As argued by Fink (21) and others this seems to be based on the differentiation of empty mycetocytes in aposymbiotic individuals and on the assumption that insects would not supply a special haven (mycetome) and mode of transmission unless they derived benefit thereform. The validity of these arguments seems open to question. A mammal reared under sterile conditions develops lymph nodes but these gradually atrophy and disappear when they are not called upon to serve continuously as an active defense mechanism; the reaction of such animals to the common intestinal bacteria supports the idea that "evolution to controlled injury" is a reality. Arthropod vectors of vertebrate disease agents sometimes transmit these microorganisms through the egg from one generation to the next in a manner comparable to the transovarial passage of beneficial symbiotes (*Babesia* in ticks). On the basis of Weyer's data (82) some strains of *Rickettsia* would be presumptuously called symbiotes today if they were not known to be related to pathogenic forms. And some of our best documented cases of mutualistic symbiosis (e.g. *Nocardia* in *Rhodnius*) show no visible modifications of the host either for abode or transmission of the microorganism (83).

We are unimpressed by the attempts to prove that cases of mutualism are evolutionarily distinct from cases of parasitism. Certainly both parasitism and mutualism have arisen many times. Whether they always arise separately, or can each arise from the other (and from commensalism) remains to be proved. Obviously, however, the negative selection value of a pathogenic organism would lead to prompt extinction of any insect strain in which a regularly transmitted mutual mutated to become harmful. It is relevant in this connection that we have recently been able by dietary means to alter either the bacteroid or its cockroach host so that the cockroach-bacteroid association becomes deleterious rather than beneficial (6). Provocative as this discovery is, it tells nothing of the origin of the association; it shows only that the association can be thrown out of balance.

Anatomical and Life History Aspects of the Host

There is a wide diversity in structure of mycetomes but nothing novel has been described since Buchner's monograph (11). The mycetome may consist of seemingly distinct cells or of uninuclear mycetocytes forming a syncytium (12). When mycetocytes are interspersed in the fat body they may be separated from one another (7) or more or less aggregated into a peripheral layer on the fat body (14).

Mycetocytes.—The mycetocytes are relatively large cells, sometimes gigantic. In keeping with the large size, they seem to be highly polyploid (15). On the basis of some chromosomal counts and then nuclear volume determinations, Baudisch (2) estimates that the mycetocytes of cockroaches range from tetraploid cells in the embryo to 256- or 512-ploid cells for some of the largest ones in adults. He suggests that the increase in chromosome number is caused by both endomitosis and nuclear fusion. An increase in chromosome number is hardly surprising. It is a common corollary of histological dif-

ferentiation in insects but its significance is unknown. When the normal development of mycetocytes is interfered with in cockroaches a few truly gigantic ones (200 times normal volume) may result (8, 9); to judge from nuclear volume (which is thought to be a reliable index) these must be highly polyploid cells. They also contain more bacteriods and are of unusual shape.

Despite occasional reports to the contrary, mycetocytes divide by a typical-appearing mitosis (15). In cockroaches, in which mitotic division was only recently discovered, it has been found that mitosis is correlated with the molting cycle. In *Blattella germanica* (Linnaeus) mitoses occur in the latter half of the molt cycle (8); in *Periplaneta americana* (Linnaeus) mitoses occur at a time when the new cuticle is just beginning to be laid down (2). Mitoses were also reported in the wood roach *Parcoblatta* (8). More than just the hormones controlling molting is involved, however, because divisions were never seen in the "empty" mycetocytes of aposymbiotic *B. germanica* or in the giant mycetocytes of experimentally produced semi-aposymbiotic individuals. It seems, then, that at least three factors are involved in mitotic divisions of cockroach mycetocytes: the molting hormone, "pressure" of an increasing population of bacteroids within the mycetocyte, and mycetocytes that are not too old.

"Empty" mycetocytes have been produced in a number of insects by experimental elimination of the microorganism [lice (64), cockroaches (7, 24, 25, 33) and several beetles (36, 72)]. In the cockroaches, Frank's photographs (24, 25) show them to be of much more nearly normal appearance in *Blatta orientalis* Linnaeus than Brooks & Richards' (7, 8) photographs show them in *Blattella germanica*. This is correlated with the fact that in *Blatta* the bacterioids were eliminated from differentiated mycetocytes, whereas in *Blattella* the transovarial transmission of bacterioids was blocked and hence these "empty" mycetocytes never had contained bacteroids.

In a scale insect, Buchner (17) has recently recorded "mycetocytes" which appear to be naturally devoid of symbiotes. Since this scale insect lives in symbiotic association with ants, Buchner speculates that the function of microorganisms usually found in this group has been replaced by secretions from the ants. Such a situation would be fine for experimental analysis but, unfortunately, these are Javanese insects and not readily handled for laboratory experimentation. In another genus, where symbiotes are found only in the female, "empty" mycetocytes are found in the male (14).

In a series of recent papers, Buchner has described situations in scale insects so amazing they would probably be doubted if reported by one less of an authority. In females of the genera *Puto* and *Macrocerococcus* the polyploid mycetocytes are reported to give rise to two visibly distinct types (15). One of these remains unchanged at the periphery of the ovary; the other divides mitotically to give smaller cells (presumably with what is called "somatic reduction") which infiltrate the ovary. These smaller mycetocytes penetrate the ovariole wall and are engulfed by the growing oöcyte. There they persist and give rise to the mycetocytes of the progeny by fusing with

yolk cells of the developing embryo (he calls this "somatic fertilization"). These mycetocytes could then be said to possess immortality in the same sense that germ cells do. In the males there is only one type of mycetocyte and they remain in the fat body as usual.

In normal cockroaches some of the mycetocytes migrate to the ovary and testes. The tropic factors involved are totally unknown but the migration is clearly a function of the mycetocyte cells themselves because "empty" mycetocytes migrate in a similar manner (7). However, dispersion of mycetocytes from an implant is very slow, and in our experiments none of the implanted mycetocytes reached and infected the ovaries (9).

Entrance of microorganisms into mycetocytes.—Normally the microorganisms become incorporated into mycetocytes at the time when these cells are differentiated by the developing embryo. The cytological and embryological pictures are quite diverse and currently unanalyzable. There may be great differences shown by even closely related species, and there is no obvious correlation to whether the microorganism appears yeast-like or bacterium-like. Commonly the form transmitted to progeny is sufficiently distinctive so that Buchner uses the term "transmission form."

More can be seen for the penetration of ovariole walls. In many cases the microorganisms pass by unknown means and routes through the follicle wall from mycetocytes adjacent thereto (7). But in some beetles Bucher (12) clearly shows them penetrating between follicular cells (this parallels the penetration of *Plasmodium* through the midgut wall of a mosquito). At our present stage of ignorance concerning the chemistry of insect connective tissue and intercellular cements, we cannot even guess how this is accomplished. In other cases mycetocytes themselves penetrate the follicle walls (presumably also between follicular cells) and after fusion pour their contents into the growing oocyte (13).

Other relations to life cycle of the host.—Sometimes, as in cockroaches, the mycetocytes persist in both sexes throughout life. In many cases the mycetomes tend to degenerate in the adult. The full range may occur within a single family of insects. Among male bostrychid beetles, Buchner (12) reports almost or complete degeneration of the mycetome in *Rhyzopertha* and *Sinoxylon*, partial degeneration in *Apate*, and no visible change in *Scobicia*.

When the microorganisms are needed in early stages it is usually assumed (and in some cases known, see below) that they supply nutritional factors for growth. An older view that intestinal ones might be involved in digestion has been largely discredited (83). When they are present in the adult it is generally assumed they are somehow needed for reproduction. Commonly they are present, and hence needed, only in the female adult. But in the German cockroach we have found them equally necessary in the male adult because aposymbiotic males mated to normal females reproduce as poorly as aposymbiotic females (7). In female cockroaches the mycetocytes infiltrate the ovary and pass bacteroids into the eggs; in male cockroaches the mycetocytes that migrate to the gonads simply lie against the testes without

visibly passing anything to them. But in both sexes bacteroid-filled mycetocytes have a great although not complete effect on fecundity.

With reproduction being affected it is not surprising that an endocrine involvement has been suggested. Wigglesworth (83) thinks that the data from *Rhodnius* imply an influence on the endocrine system, and compares the fate of aposymbiotic individuals to an experimentally produced diapause. Frank (25) likewise suggests a hormonal relationship but without presenting convincing data for it. In contrast, our data from successful mycetocyte transplantations into aposymbiotic cockroaches showed no hormone-like effects in this species (9). If there is an endocrine involvement it would almost certainly be indirect, i.e. the symbiote affects some part of the metabolism, which in turn affects the endocrines, which in turn affect the insect: Or, for the cyclic and sexual polymorphic forms shown by some symbiotes, the endocrines affect the internal environment which in turn affects the symbiote (19, 44). The suggestion by Musgrave & Miller (54) that the mycetomes are endocrine glands secondarily invaded by symbiotes does not warrant serious consideration in the total absence of supporting data.

A unique and amazing situation has recently been described by Buchner (13, 14) for the coccid genus *Stictococcus*. *Stictococcus diversiseta* Silvestri has yeast-like organisms in its mycetocytes; *Stictococcus sjoestedti* Cockerell has bacterium-like ones. In both, mycetocytes invade the ovary but by chance infect only certain oöcytes (those adjacent to which they come to lie). Two types of eggs are thereby produced, one infected, one uninfected. These develop parthenogenetically. Infected eggs give rise to females, uninfected eggs give rise to males. Since cytologists have shown that production of males in this group involves loss of a chromosome, it follows that this is the gross mechanism for the action. But how the presence of symbiotes prevents this loss or the absence of them causes it is a mystery. With the same result being produced in one genus by two so different-looking microorganisms we are led to wonder if this case may not be in the nature of a stimulus-response reaction rather than the microorganism supplying some needed chemical.

Elimination of the Symbiotic Microorganisms

Methods.—There is no one universally applicable method for eliminating the symbiotes. In cases where the symbiotes live in the gut lumen and are transmitted to the progeny as contaminants their elimination may be easy. Their transmission is so readily interrupted in *Rhodnius* that the symbiotes may be lost by keeping the breeding cages too clean or rearing the bugs in semi-isolation (1, 83). In other cases where transmission is by contamination of the outside of the egg shell (as in the beetles *Lasioderma* and *Stegobium*), elimination is readily accomplished by surface sterilization of eggs followed by rearing away from sources of reinfection or by the manual removal of symbiote packets from the egg masses (53). For the intestinal protozoa of termites and the roach *Cryptocercus*, high oxygen tensions are fully effective within an hour or two (56). In a variety of cases (beetles, coccids and

cockroaches) elevated temperatures just sublethal for the insect kill the symbiotes to a greater or lesser degree (7, 21, 31, 36, 72). Unfortunately this method kills many of the insects and gives erratic results. However Schneider (72) presents data supporting the earlier suggestion by Koch that natural high temperatures of the tropics have been a cause of the development of asymbiotic strains of *Sitophilus granarius*. Other naturally occurring asymbiotic strains of this species have been recorded from Canada by Musgrave & Miller (55). Displacement by centrifugation or extirpation gives aposymbiotic human lice (64). Temporary starvation has been reported to be effective with *Pseudococcus citri* (Risso), (21), and while details are still being investigated, we have found that diets inadequate because of the kinds of salts present can yield aposymbiotic cockroaches (6).

In a number of cases no method has yet been found for eliminating the microorganisms (*e.g.* 75).

Most provocative, however, are the recent successful attempts at eliminating intracellular symbiotes by the administration of antibiotic drugs to the host insect. These successes may be cited as evidence that the supposed symbiotes are actually microorganisms; but, as pointed out by Lederberg (51), they can hardly be considered proof when similar treatments can be used to eliminate chloroplasts from plants. More importantly, these drugs in at least some cases provide a reliable method for elimination of intracellular symbiotes which are transovarially inherited, and hence provide aposymbiotic individuals for study.

With the cockroach *Blattella germanica*, Brooks (4, 7) found that the addition of chlortetracycline (aureomycin) to the diet at a concentration of 0.1 per cent resulted in destruction of the bacteroids inside growing eggs and hence resulted in obtaining aposymbiotic progeny. Sulfathiazole resulted in offspring some of which were normal and some aposymbiotic. With the cockroach *Blatta orientalis*, Frank (24, 25) independently and simultaneously reported elimination of bacteroids from the mycetocytes by injection or feeding of penicillin, chlortetracycline, or oxytetracycline (terramycin). The latter author obtained only erratic and partial elimination with high concentrations of the drug chloramphenicol (chloromycetin).

But there are startling differences in these two cases. With the German cockroach fed aureomycin at a low level continuously, survival and reproduction of the treated generation were excellent, the symbiotes were eliminated only from oöcytes at the stage of rapid enlargement, and the aposymbiotic individuals obtained were not the treated individuals but progeny of the treated individuals. With the oriental cockroach, where larger doses were used for shorter periods of time, survival was less good and reproduction was very poor, but the symbiotes were apparently eliminated from the mycetocytes and hence the aposymbiotic individuals were the treated individuals (the few progeny obtained were also aposymbiotic). We have unpublished data which suggest that experiments on the American cockroach will be found to agree with those on the oriental cockroach. (In this case the dosage

of antibiotic is quite critical because there is only a slight difference between the amount needed to eliminate the bacteroids and the amount that is lethal for the cockroach.)

The antibiotic effect of aureomycin and chloromycetin in German cockroaches is potentiated by adverse salt concentrations (6). Concentrations of these antibiotics, which have no noticeable effect when mixed with the dog biscuit food, can prevent transmission and even block tetrazolium reduction by bacteroids in the fat body if Wesson's salt mixture is used in the diet. This synergistic effect of salts on the action of antibiotics concerns both the bacteroids and reproduction of the cockroaches.

Geigy *et al.* (27) used chloramphenicol, chlortetracycline, and oxytetracycline on the bug *Triatoma* and report that only oxytetracycline was effective for elimination of the gut symbiotes.

Effects of eliminating symbiotes.—These are usually considered to reveal the effects of the symbiotes on the host, and the elimination of symbiotes is our principal method for studying the effect of the symbiotes. Of the many hundreds of symbiotic associations that have been described (11), there are only a little over a dozen for which aposymbiotic individuals have been studied. Koch (46, 47) has recently reviewed this literature more extensively than space will permit here.

In one case (*Rhyzopertha*) aposymbiotic individuals appeared completely normal, *i.e.*, no effect of the symbiotes was found (36). In another case (*Sitophilus*) the aposymbiotic individuals are simply smaller and lighter in color, comparable to individuals reared under suboptimal conditions (72). Aposymbiotic individuals of the bugs, *Triatoma* and *Coptosoma*, suffer increased mortality and prolonged developmental time (26, 53), whereas *Rhodnius* is more seriously affected and only rarely metamorphoses to the adult stage (1, 83). In the best analyzed cases (*Lasioderma* and *Stegobium*) it has been found that the symbiotes supply most of the B vitamins and sterols, and that, accordingly, the nutritional requirements become more stringent in the absence of the symbiotes (58). These data have been reviewed extensively in various publications in recent years (52) and will not be reiterated here. Various comparative discussions of the role of symbiotes suggest that they usually function by making marginal or submarginal diets adequate (11, 23, 42, 44, 45, 47). It follows that demonstration of a beneficial role for symbiotes may commonly require placing the aposymbiotic insect under stress. In other words, aposymbiotic and symbiotic individuals may live equally well under optimal conditions and yet not live equally well under particular suboptimal conditions. In effect, this is what Huger (36) suggests but does not demonstrate in the case of *Rhyzopertha*.

It is possible that in some special cases symbiotes may be involved in digestion. Thus, Rybicki (70) thinks that the intestinal flora is responsible for digestion of wax by wax moth larvae (*Galleria*), and Florkin (22) suggests that in general the digestion of resistant compounds such as wax, cellulose, and chitin by animals involves intestinal bacteria. More definite in this

connection is the intermediation of intestinal microorganisms in the utilization of cellulose by termites, although it is still uncertain how much of this is done by the protozoa and how much by the bacteria that are present (71). However, a *Ctenolepisma* has recently been reported as digesting cellulose without the aid of microorganisms (49a).

Another special case involves the fixation of atmospheric nitrogen. For years, Tóth (78 to 80) has been amassing data on this subject. Experiments with cultured symbiotes seem to document conclusively that these organisms can fix nitrogen, and utilize ammonia even better (21, 61), but attempts to demonstrate that they do a significant amount of this when in an insect have given negative results. Even studies using tracer nitrogen have failed to show its utilization in the insect. More recently Tóth (80) has emphasized that nitrogen-fixing bacteria from various sources do not fix nitrogen except in the absence of bound nitrogen. They are said to liberate nitrogen from urea and uric acid. The phenomenon could then be important only under conditions of extreme nitrogen deficiency—a condition not likely to be found in a symbiotic association.

An involvement in the nitrogen economy of the insect is still possible. Tóth (80) is now suggesting that the symbiotes decompose uric acid, perhaps even utilizing the ammonia released for the synthesis of protein. This suggestion is consistent with the observation that aposymbiotic cockroaches contain larger accumulations of urate crystals than normal individuals of the same age (9, 25). Direct quantitative study of this point could easily be done now with cockroaches (and should be done).

In other cases it has not proved feasible to perform definitive experiments [e.g., scale insects which cannot be fed artificially (21)]; or, still undiscovered factors prevent saying more than that the symbiotes supply vitamins and something else. Thus, aposymbiotic human body lice, which are difficult but not impossible to feed artificially (30), can be grown better on addition of yeast; a certain percentage of the males reached maturity for Puchta (64, 65) and appeared to be normal, but the few females were short-lived and failed to reproduce. Similarly, with the blood-sucking bug *Rhodnius*, Baines (1) shows that B vitamins and something else is needed for metamorphosis and reproduction. Further study of these cases is highly desirable, and, we trust, will be forthcoming.

The recent successful elimination of bacteroids from cockroaches has provided us with one of the best cases for further analysis. This is additionally interesting as a case where the presumed microorganisms (bacteroids) are intracellular in specialized mycetocytes. In *Blatta orientalis* as described by Frank (24, 25) the aposymbiotic individuals are 40 per cent smaller than normal, of lighter color, and even though they grow on fortified diets they do not equal the growth of normal individuals and there is almost no development of eggs. Data from such individuals have an uncertainty due to the fact that the aposymbiotic individuals were all treated with antibiotics and hence it is uncertain how much of the observed effect is due to the drug and how much to the absence of bacteroids. In *Blattella germanica* the data

by Brooks (4 to 9) suggest we have a nearly ideal experimental animal. It is large enough for experimental manipulation, has a reasonably short life cycle, and the bacteroids can not only be eliminated by a variety of diverse methods (antibiotics, diet or heat) but aposymbiotic colonies can be established. This makes it reasonable to assume we are really dealing with the effects of aposymbiosis. Convincing documentation that the effects are due to aposymbiosis comes from recovery of growth and normal color following implantation of fat-body containing mycetocytes from normal donors.

Aposymbiotic German cockroaches grow slowly on diets fortified with yeast or lyophilized liver to give adults that are small, light-colored and of reduced reproductive capacity. Analyses with synthetic diets have shown that the bacteroids can supply the insect with B vitamins, amino acids and some larger protein fragment that may be a tripeptide (since casein of the synthetic diet is not adequately replacable by hydrolyzed casein or known amino acid mixtures) (5). A provocative fact is that the reproductive power (both in males and females) is not just reduced but is nearly limited to older adults. Conceivable explanations of this fact include the idea that the bacteroids make up the amount of deficiency in some one or more metabolites rather than supplying something otherwise totally lacking; in other words accelerate metabolism rather than supplying an absent compound. Or, they regulate the metabolic balance in some other way such as Puchta's suggestion (65) that the symbiotes supply vitamins in "proper dosage." (This could well be important because the nutrition literature shows that optimal growth requires not only that certain ingredients are present in the food but that they are in certain ratios to one another.)

The lighter color of aposymbiotic cockroaches has not been recorded in detail. The color that does develop, occurs at the usual time. Serial sections show no significant differences in thickness of the cuticle or its component parts. The only difference is in the intensity of color in the thin exocuticle. The effect, then, seems to be entirely on the tanning or sclerotization reaction which is simply of lesser intensity.

To summarize on this topic, it is well documented that in certain cases the symbiotes supply B vitamins under conditions approximating normal, and that in other cases they supply more than this. What more they supply remains to be determined, but it is difficult to conceive of internal microorganisms providing any useful service to the insect host other than providing or assisting in some chemical process involved in metabolism. With the possible exception of sex determination in *Stictococcus* (see preceding section), all of the data imply nutritional involvement, or a reproductive involvement that likely has a metabolic basis (perhaps including hormone production), or other metabolic steps such as the possible mobilization of urates.

The Microorganisms

Properties of the supposed microorganisms: The microorganisms may appear microscopically similar throughout a taxonomic group. Thus Buchner

(12) records similar cyclic changes which he interprets as indicating closely related bacteria in various genera of bostrychid beetles. In contrast he (14) records that one species of the coccid genus *Stictococcus* has intracellular yeast-like organisms whereas a second species has bacterium-like ones. Obviously no generalizations can be made. Sometimes more than a single supposed symbiote is found in a host (11).

The symbiotes, especially those living free in the lumen of the gut or in a mycetome, may be readily cultivatable and hence are indubitable microorganisms. In other cases, such as the bacteroids of cockroaches, they may be refractory to cultivation and yet certainly appear to be microorganisms (remember that three large groups of parasitic fungi have never yet been cultured despite repeated attempts: the rusts, powdery mildews and Laboulbeniales). But there are also cases where the supposed organism is refractory to cultivation and of decidedly dubious status in nomenclature. This is illustrated by the recent Lanham-Trager controversy (49, 81) in which, to our way of thinking, Trager had so much more cogent an argument that Lanham's ideas seem untenable. However, few, certainly not the present reviewers, would care to go to the extreme represented by Peklo (60) who would class many cellular particulates (including the sarcosomes of muscle!) as symbiotic microorganisms simply because they look similar to things he can grow in culture. So little detail can be seen in these minute bodies that microscopic similarity seems to us of little significance. Many of the identifications in the literature are clearly subjective guesses of observers with varying degrees of experience (59). Published illustrations commonly show nothing distinctive. Perhaps these identifications based on interpretation of inadequate morphological data may be correct in the majority of cases but some supposed symbiotes examined in connection with classroom teaching have impressed us as more likely being granules belonging to the insect's cells.

The question, then, of what is to be considered adequate documentation arises. When is what we find in an insect really a symbiotic microorganism? Obviously adherance to Koch's postulates is desirable (Lederberg (50) chides entomologists for usually ignoring these) but complete orthodoxy has seldom been possible because of the inadequacy of our techniques except for organisms living in the gut lumen (27, 56, 58, 83). In the absence of data on cultivation and on reinfection of aposymbiotic individuals, evidence may be claimed from histochemical tests, from cyclic changes of the supposed organism, from their transfer to oöcytes, and occasionally from other properties. Taking the bacteroids of cockroaches as an example; some authors claim to have cultivated these (38, 39, 62) but the morphological identification of the cultured organisms is, to say the least, open to question, and it has not yet been possible to prove the cultures by reinfecting cockroaches. The bacteroids are both gram positive at certain stages and Feulgen positive. Equally suggestive, Brooks showed (4) that appropriate staining revealed typical filamentous mitochondria in the mycetocytes in addition to

the bacteroids (which do not stain like mitochondria), and that cell fractionation with centrifugal separation of the bacteroids showed them far more resistant to dissolution than mitochondrial preparations are. Also, they are passed into oöcytes and can be followed through embryonic development during which time they seem to become incorporated only into the future mycetocytes. And finally they can be eliminated by treatment with certain antibiotics. We believe that these bacteroids are obligatorily symbiotic microorganisms but we would not claim that this has been proved.

Histochemical properties.—These have not been examined exhaustively for any species. Perhaps the most data are available for the bacteroids of cockroaches. The bacteroids are gram positive or negative depending on the stage (25, 62); they give a rather diffuse Feulgen DNA reaction (4, 25, 69); they stain with Giemsa and haematoxylin but not with Sudan dyes, with the Baker acid hematin test for phospholipides, or the periodic acid-Schiff reaction for polysaccharides (4); they are not detectably fluorescent or birefringent (4); and they give an intense reduction of neotetrazolium (4). The neotetrazolium reaction, however, showed some peculiarities that we did not satisfactorily work out (e.g., inhibition by α-ketoglutarate). Electron microscope examination by de Haller (33) revealed neither cilia nor capsules.

The symbiotes of the bedbug have been reported to be Feulgen positive (20), those of the human louse to be stained by Giemsa and methylene blue only at certain stages (67), and those of *Rhodnius* to be gram positive (1).

Polymorphism: Space will not permit descriptions. Many descriptions and figures are to be found in Buchner's monograph (11) and an interesting more recent review is given by Koch (44). Polymorphic forms or cycles have been described for symbiotic bacteria, yeasts, filamentous fungi and protozoa in insects.

In cultures the yeast (*Candida*) from cerambycid beetles varies visibly with the kind of sugar in the medium. Gräbner (28) obtained forms similar to what one sees in the insect only when xylose was included (this sugar also gives particularly rapid growth). The yeast from *Sitodrepa* can utilize more kinds of sugars than the yeast from *Ernobius* but it does not ferment any of them. Puchta (67) describes changes in form of louse symbiotes as a function of the medium, and Kotter (48) describes stains based on the ability to ferment sugars. With the filamentous bacterium from *Rhodnius*, Baines (1) describes development from filaments to fragments to cocci (or chains) similar to the cycle seen in the bug.

Commonly, polymorphism is shown within the insect as well. The types may occur in the mycetome or gut as a regularly-repeating cycle correlated with the stage of the insect (12, 19, 21, 28, 67), and may be different in the two sexes (67). In beetles, Gräbner (28) reports that the intracellular yeasts all stain alike in any one mycetocyte but differently in different mycetocytes (he recognized three staining types). Since the development of the insect is under hormonal control, it is not surprising that hormone involvement, presumably indirect, has been suggested (19, 44). Of considerable potential

interest is the fact that several authors refer to special "transmission forms" for infection of the oöcytes (12, 67). Perhaps this implies that the reinfection of aposymbiotic individuals will require not only development of a technique for reimplantation but also use of the correct stage of the symbiote. Unusual changes in form, and staining reactions, are sometimes seen following experimental treatments (4, 9, 24).

The culturing of symbiotes.—Cultures of yeasts have been grown from some species of beetles but not from others (28, 57). Obviously the culture requirements vary (and obviously several genera of yeasts are involved) (28). The bacterium, *Nocardia rhodnii*, has been cultured quite successfully (1), as have also the bacteria from other bloodsucking bugs (27). The above are particularly interesting because cultures of several of them have been used successfully to reinfect aposymbiotic individuals (1, 2, 27, 53, 58, 83). Culturing of several other bacteria has been recorded (21, 34, 38, 39, 48, 61, 62, 63, 67, 76, 79, 80). Survival of the bacteroids of the German cockroach in extirpated tissue after the degeneration of the host cells has been reported by de Haller (32).

To the present reviewers major interest centers around three sets of observations. Gräbner (28) could cultivate the yeasts from anobiid beetles only when he started with a massive inoculation; in agreement with this he found that all the yeast symbiotes he studied released "growth substances" into the medium. Fink (21) was able to obtain cultures of *Mycobacterium dactylopii* from coccids only when other microorganisms were present (kept separate by dialysis membrane); after this initial "nurse culture" was well established it was possible to obtain pure cultures by subculturing. And, finally, Ketchel & Williams (39), in claiming to have cultured the bacteroids of cockroaches, report that their initial cultures contained both a yeast and a rod-like bacterium in addition to the diphtheroid they thought to be the bacteroid; in other words, they too, albeit inadvertently, started with a mixed culture.

We interpret the data in the last paragraph as indicating that the cultured organisms in these cases are not physiologically the same as the symbiotes *in situ* in the insect. Whether they have changed by adaptive mutation or in some other way, i.e. whether the change is permanent or not, they still are only questionably equal to what one finds in the insect. Such data lead us to wonder how much reliance can be placed on *in vitro* data in interpreting *in vivo* relationships. Actually this situation is not surprising. It is well known that many parasites are capable of doing things other than what they usually do, and that free-living organisms will live successfully in the laboratory under conditions simulating ones in which they are never found in nature. In fact it has become almost routine to check laboratory ecological data against field data because organisms can do so much more than what they usually do in nature. So too, data from cultured symbiotes (or parasites) show only what these organisms can do; separate documentation is necessary to show what they actually do when in another organism.

Several examples could be cited in support of the above point of view. For instance, there is the mass of data on fixation of atmospheric nitrogen (80), and the report that while the symbiotes of *Triatoma* synthesize folic acid (3), the aposymbiotic larvae of these insects are not aided by the addition of folic acid to their food. And the microorganisms, surprisingly, are said to synthesize this vitamin as well in the presence of aminopterin, a folic acid antagonist, as in its absence (26, 27).

Perhaps because we are entomologists rather than microbiologists it seems to us that the chief importance of culturing symbiotes is to document that we are dealing with living organisms rather than cellular products. Determination of the nature of the symbiotic relationship requires other approaches.

Effects of the insect on its symbiotes.—Presumably, at least the cyclic and sexual changes treated in the section on polymorphism represent effects of the insect. In the case of internal symbiotes the insect is the environment of the microorganism, and changes other than normal growth can be said to reflect the environment.

A beautiful story on the sexual cycles of protozoa in termites and *Cryptocercus* has been developed by Cleveland & Nutting (19). These cycles vary from one species of protozoan to another but are always precisely related to the molting cycle of the insect. Since molting is controlled by hormones these cycles are likewise controlled by the endocrine mechanism of the insect (56). Cleveland & Nutting speculate that the control is direct, but we would rather guess that it is indirect by the hormones affecting the gut epithelium, which in turn modifies the chemical composition of the gut lumen, which in turn affects the protozoans.

It seems obvious that the insect must be a favorable environment (10). In some cases symbiotes are lost from the gut lumen at the time of molting; provision in terms of habits of the insect must be made for reinfection (56).

But can a living insect become an unfavorable environment for its normal intracellular symbiotes? Obviously this happens as a function of age in those many cases where the symbiotes disappear in the adult. We have found that this situation can be produced experimentally with cockroach bacteroids even without the use of antibiotic drugs. Diets deficient in manganese result in a loss of the bacteroids (6). Other deleterious changes have been found which will be treated in the final section of this review.

It is routinely assumed that the microorganism derives benefit from being in the insect. Our ideas on this point are largely logical deductions from the fact that the microorganism persists and reproduces and is not known to occur elsewhere in nature. It does seem reasonable to argue that the microorganism obtains or at least may obtain more kinds of advantages than its host. The advantages to the host can be thought of exclusively in terms of metabolic events. The advantages to the microorganism certainly include metabolism; at least in the sense that all organisms derive metabolic precursors from their environment. But the microorganism derives other things

commonly classified as benefits. It obtains a favorable abode, protection from desiccation, geographic dispersion, etc.

The Specificity of Symbiotes

Extremely little information exists on this subject, and this state of affairs will continue as long as most of the workers in the field give little heed to Koch's postulates. We agree emphatically with Lederberg's criticism that "too little emphasis has been placed on the occurrence and behavior of 'disinfected' or aposymbiotic individuals, and on the criterion of reinfection for the specificity and identity of the endosymbiotic microorganism" (50). But at present no technique exists for reinfecting, and hence testing the specificity of symbiotes which are transmitted to progeny via cytoplasm of the egg. The only tests have been with microorganisms that live in the lumen of the gut.

Pant & Fraenkel (58) showed that yeasts from the beetles *Lasioderma* and *Stegobium* could be interchanged. These, then, are not host specific. To judge from growth rates of the insect, the yeast from *Lasioderma* is more efficient. In a very interesting study, Nutting (56) reported that the various intestinal protozoa of termites and *Cryptocercus* can be interchanged. The insects (especially the termites) grow quite satisfactorily but the protozoa tend to abort at the stage of sexual reproduction. Transfaunation, then, is possible but the new association is not a completely harmonious one.

We have made transplants of fat body containing mycetocytes from one species of cockroach to another (from oriental and American cockroaches into aposymbiotic German cockroaches). The implants survived for days or a few weeks but eventually degenerated after apparently losing the bacteroids from the mycetocytes (9). These experiments, however, as well as de Haller's (33) grafts of fat body of the German cockroach in other orthopteran families, tell nothing about the specificity of the bacteroids themselves.

A different level of nonspecificity is shown by Puchta's (66) report of growing beetle yeasts intracellularly in chicken fibroblasts in tissue culture. Various nonsymbiotic bacteria did not behave in this manner.

The Balance of Host and Symbiote

Buchner and his associates frequently emphasize and even insist that an insect and its symbiotes comprise a biological unit (10, 21, 45, 65). We concur completely with this point of view. The idea restated in ecological terminology is that all mutualist-host (and parasite-host) relationships are ecological associations differing from other microcommunities in that the association is not only obligatory for at least one of the members but that means of perpetuating the association (=transmitting the microorganism to progeny) have also been developed. Disruption of the association changes the ecological requirements of the partners. The unit in nature, then, is the symbiote-host.

This association must be dynamically balanced and must remain bal-

anced. Three sets of experimental data bear on this point. Puchta (65) reports that blood containing overdoses of B vitamins or yeast extract is injurious to *Pediculus*, and, more significantly, that it is especially and quickly injurious to normal lice in contrast to aposymbiotic ones. Brooks (6) reports that the salt composition of cockroach diets is not only important to the insect but somehow changes either the host or symbiote or both such that the previously beneficial association becomes deleterious (Mn, Zn, and the Ca/Zn ratio are the important elements). One could interpret these results as showing that the originally mutualistic bacteroids have become pathogenic (a common attribute of parasites but one that in a mutualist host relationship would quickly lead to extinction). The above two cases agree in showing deleterious results from alteration of the host-symbiote balance. The two cases differ in that the first deals with the effect of unbalanced food (metabolic precursors) on normal insects, the second deals with normal food on an altered host-symbiote.

One could classify the possible methods for studying this relationship as: (*a*) growing symbiotes in pure culture, (*b*) producing aposymbiotic hosts, (*c*) altering the relationship by changing one or both partners, and (*d*) developing artificial symbiosis. The last set of data to be discussed is Puchta's attempt to develop artificial symbiosis. He (66) grew yeasts from the beetle *Rhagium inquisitor* (Linnaeus) and various nonsymbiotic microorganisms in the presence of fibroblasts from chicken heart (tissue culture). The beetle yeasts grew moderately well and even became engulfed to give an intracellular association. He concluded that the results indicated no more than a commensal relationship, but we wonder how much more he could hope to show when dealing with optimal or at least not deficient media. The results obtained so far are more provocative than informative. It is to be hoped that this approach will be pursued further.

Concluding Remarks—Largely Warnings

For others contemplating work in this field it might be helpful to list some of the pitfalls likely to be encountered. Some of these have already been remarked on in preceding sections. Two we will repeat: many authors imply that "symbiote" equals "mutualist," and most authors ignore Koch's postulates (50, 51).

Smears from biopsied material are likely to be a woefully inadequate criterion of infection. We have found that with a considerable reduction in mycetocyte population smears usually give negative results although complete sets of serial sections show some bacteroid-containing mycetocytes still present (7). Even a negative verdict from complete sets of sections indicates only failure to find symbiotes. The most reasonable explanation of the "loss" of our aposymbiotic roach colony after eight to ten generations is that a few unrecognized bacteroids are transmitted (the presence of masked or otherwise unrecognizable forms is also possible) and eventually repopulate the persistent mycetocytes. The bacteroid-containing roaches, being healthier

and faster-growing, quickly displace the aposymbiotic individuals in the colony. If this suggestion is correct, then we probably never have had truly aposymbiotic populations but only ones grossly deficient in bacteroids.

Numerous experiments in the literature are difficult to compare because of differences in the end-points chosen by the experimenter (growth, color, wing formation, fecundity, survival of F_1, etc.). Reproductive capacity can be especially misleading if only negative results are obtained. It is known that not only does egg-laying vary as a function of the mother's age, but the quality of the eggs laid can also vary (68). In establishing our aposymbiotic colony of German cockroaches we found that the first few egg capsules were regularly aborted and that viable eggs were obtained only when we managed to keep the adults alive to a relatively old age. And more than just the antibiotic may be involved because we find that inorganic salts in the diet can act as synergists potentiating the effect of the drug (6).

Surveying the literature, one is impressed by the different results reported by various authors (compare 7, 25, 31). This suggests that the problems are complicated by physiological strains, diet and precise methodology, a point readily illustrated at the comparative level by the striking differences between *Blatta* and *Blattella*, and at the specific level by the effects of dietary salts in *Blattella*.

Further developments will depend in large part on more diligent work on the species already studied. The antibiotics provide us with a most important research tool, but we think that advances in our knowledge will come from the study of the aposymbiotic individuals made readily available rather than from the antibiotic effect itself. Several suggestive developments have occurred more recently but it remains to be seen how productive of useful information they will be. Puchta's "artificial symbiosis" approach is provocative (66) and Brooks' nutritional approach to the alteration of the partnership balance (6) seems even more promising. We should continue to watch for novel approaches and favorable experimental animals.

As a concluding remark, we suggest that endomutualism and endoparasitism must have much in common. Despite the Buchner-Koch-*et al.* philosophy that these cannot be evolutionarily related (44)—a view we neither accept nor decline—it would seem that students of both mutualism and parasitism could profit from the findings of the other. It could well be that there is no sharp distinction, and that the differences are only of degree (involving metabolic balances, mode of transmission, and production or nonproduction of injury or injurious compounds). Certainly either parasite or mutualist would be classed as pathogen as soon as it began to produce significant injury.

Addendum: Since this article was written, one of us (A.G.R.) had the opportunity to spend two days with Professor P. Buchner examining his slides pertaining to symbiosis in coccids. Astonishing as his reports may sound, they are well documented by his preparations. However these phenomena are to be explained, there is no question in the minds of the authors of the correctness of Buchner's reports.

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NUTRITIONAL REQUIREMENTS OF PHYTOPHAGOUS INSECTS[1,2]

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In this review the term *phytophagous insect* is restricted, with few exceptions, to insects that customarily eat only fresh plant material. Lack of space prevents inclusion of many interesting papers on feeding behavior, food utilization, work with natural and semisynthetic diets, and other studies pertaining to nutrition. This review is restricted to a critical appraisal of the nutritional requirements of phytophagous insects and of some of the speculations that have been made regarding the part that these requirements play in the relationship between the insects and their host plants. Reviews of insect nutrition giving much broader coverage are available (23, 25, 55, 72, 73, 103, 104, 105, 115).

Beck (14) succinctly defines nutritional requirements as "chemical factors essential to the adequacy of the ingested diet" chemical feeding requirements, as "chemical factors important to normal feeding behavior"; and physical feeding requirements, as "dietary texture, position, light intensities and other physical factors influencing feeding behavior." These terms are used throughout this paper as Beck defined them.

An attempt was made to include all works that give direct proof of the nutritional requirements of phytophagous insects for specific chemicals. The most striking feature of the field is that little definite information is as yet available. Trager's review (103) in 1947 stated,

> Because of the difficulties attending nutritional work with large groups of leaf-feeding and parasitic insects, it has not yet been possible to obtain information concerning the chemical nature of their specific nutrients.

The exhaustive tabulations of Albritton (2) summarize the knowledge of this subject up to 1954, giving reports on carbohydrate utilization in eight phytophagous species and showing that larvae of the European corn borer, *Pyrausta nubilalis* (Hübner), require fatty acids, cholesterol, choline, and an unknown factor.

The main barrier has been lack of suitable chemically defined diets and aseptic rearing techniques. To determine the specific nutritional requirements of an organism one should know the chemical composition of the diet and should be able to change the constituents and prepare various diets precisely. Microorganisms must be excluded from the experiment because they can produce dietary factors and can change the composition of the diets, thus ruining the significance of the nutritional test. Since the chemical composi-

[1] The survey of literature pertaining to this review was completed in April, 1957.

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tion of plants can be controlled only very slightly, the exact nutritional requirements of plant-feeding insects must be determined with artificial diets. Ideally, these diets should enable normal development of the test insect for many generations.

Devising a suitable chemically defined diet for a phytophagous insect is difficult since it must satisfy the insect's requirements for physical and chemical feeding factors, be in an edible physical form, and contain the correct amounts of the essential nutrients. Problems in the formulation of such diets have recently been discussed (40). Formulating the diets has been further complicated by the observation that the dietary requirements for sugar and protein may change during the larval period (14). Chemical diets and aseptic techniques have thus far been used for larvae of four phytophagous species, namely, the European corn borer, *P. nubilalis* (9 to 12, 16); the pink bollworm, *Pectinophora gossypiella* (Saunders) (107 to 110); the Asiatic rice borer, *Chilo suppressalis* (Walker) [= *C. simplex* Butler] (56, 60, 63, 65); and the onion maggot, *Hylemya antiqua* (Meigen) (41, 42, 43). Most of the knowledge of the nutritional requirements of phytophagous insects has come from these experiments. Phytophagous larvae are inefficient in converting food into body tissues (104), but the following sections show that their requirements for carbohydrates, amino acids, lipides, vitamins, minerals, water, and other dietary factors are rather similar to those of other insects.

Carbohydrates

Dietary carbohydrates are used principally as sources of energy and for fat and glycogen synthesis. Sugars constitute the sole food of certain adult insects and may play a role in feeding behavior (12, 15) and in orientation of certain phytophagous insects on the host plants (13, 33). It is generally considered that carbohydrates are always broken down into their component monosaccharide units before they are absorbed by the insect gut (111). Carbohydrates that cannot be broken down or absorbed will not satisfy the insect's dietary requirements. Some carbohydrates are unacceptable because of taste and some are toxic (39). The technique of rapid paper chromatography of carbohydrates and related compounds described by Gordon *et al.* (50) should be useful in future work on carbohydrate requirements of insects by providing easy chemical identifications of these compounds.

The major carbohydrate of the blood of a species of silkworm, *Antheraea polyphemus* (Cramer), is trehalose, a nonreducing sugar. This finding demonstrates that estimating the carbohydrate content of insects in terms of glycogen and reducing sugars is not sufficient (117). Trehalose was also found in all other insect species examined, which included representatives from five orders (117).

Polysaccharides.—Lack of the necessary digestive enzymes prevents many species of plant-feeding insects from utilizing the cellulose in their diets. The lack of cellulose-splitting enzymes does not mean that only the contents of masticated cells are available as food. Larvae of *Phalera bucephala*

(Linnaeus) absorb more than half of the protein, fat, and sugars from swallowed leaf tissue consisting largely of unbroken cells (35). Parkin (85) has reported similar findings with *Lyctus* sp. The digestion of cellulose by insects has been admirably reviewed by Day & Waterhouse (29), and the relationship between termites and other wood-boring insects and various cellulase-supplying microorganisms is classic (29, 106, 115).

Phytophagous insects vary in their ability to utilize starch. Larvae of *Malacosoma neustria* (Linnaeus) can probably use the starch present in their diet, whereas those of *Aglais urticae* (Linnaeus) and *Pieris brassicae* (Linnaeus) cannot. None of these three species can utilize cellulose or hemicellulose (36). Larvae of *Prodenia eridania* (Cramer) cannot utilize the starch present in young bean leaves although the larvae have a starch-splitting enzyme (27). Brown (21), testing *Melanoplus bivattatus* (Say), concluded that intact starch grains are unassimilable and that this grasshopper is a wasteful feeder as regards polysaccharides. The larvae of *Automeris io* (Fabricius) cannot utilize the starch in their natural food (22). Tsutsi & Saito (105) considered that *C. suppressalis* larvae can utilize starch after the first instar. Hirano & Ishii (56) showed that larvae of this species utilize glycogen more readily than starch and that inulin in the diet as the sole source of carbohydrate will not support larval development.

Sugars.—The dietary requirements for sugars are nonspecific but certain sugars are utilized more readily than others. Albritton (2) gives data on sugar utilization for eight species of phytophagous insects. The recent review of Lipke & Fraenkel (73) also contains many reports on the subject. Frings (44) was unable to show a rejection threshold for glucose, sucrose, or lactose in *Hyalophora cecropia* (Linnaeus)when these sugars were presented in solution on leaves of the sycamore *Platanus occidentalis*. The insect's requirement for sugar may vary with larval age. Larvae of *P. nubilalis* do not require dietary glucose until the fourth instar; however, a glucose level of 18 mg. per gm. of artificial diet allowed apparently optimum growth (14). Feeding-preference experiments with different concentrations of glucose, fructose, and sucrose, the principal sugars of the corn plant, showed that the first-instar larvae tested singly under artificial conditions in a simplified environment were extremely sensitive to differences and selected the highest concentration offered (12). This insect displays a bimodal response to different concentrations of these three sugars. Larvae tended to prolong their feeding as the sugar concentrations were increased in the simple artificial diets used, and the spectrum of response towards these sugars was very similar to the human taste spectrum for sucrose (15). Of the carbohydrates present in their natural food, larvae of *Automeris io* (Fabricius) utilize only the hexose reducing sugars and disaccharides (22). The soluble sugar content of plants may limit reproduction and development of winged forms in the aphid *Brevicoryne brassicae* Linnaeus (34). The pentoses or pentosans in the bean *Phaseolus vulgaris* may inhibit the growth of the weevil *Callosobruchus chinensis* (Linnaeus) (61). The leafhopper *Circulifer tenellus* (Baker) survived approxi-

mately 312 hr. when fed through a membrane on aseptic 1.5 per cent glucose or fructose solution and synthesized fats during this period (46). Sucrose is utilized more readily than glucose by larvae of *Malacosoma neustria*, *Aglais urticae*, and *Pieris brassicae* that have been fed willow, nettle, and cabbage respectively (36). Hirano & Ishii (56) tested the nutritive value of many carbohydrates for the aseptic growth of larvae of *C. suppressalis* on chemical diets. On the basis of a 35-day assay period they rated the monosaccharides tested in the following order: fructose > glucose > galactose = manose = sorbose > rhamnose = xylose > arabinose > ribose; and the oligosaccharides as: maltose = sucrose > trehalose > raffinose = melezitose > melibiose = lactose > cellobiose.

Proteins and Amino Acids

No one has yet shown that any phytophagous insect requires specific proteins or polypeptides. Whether the proteins occurring in plants must be reduced to their component amino acids before absorption by the insect's gut is not yet known (111). Experiments with chemical diets have demonstrated that free amino acids can be absorbed and utilized. *Prodenia eridania* larvae utilize most of the protein in the leaves they eat (27). The phytophagous insects studied thus far have shown the same requirements for amino acids as the rat. Arginine, histidine, isoleucine, leucine, lysine, methionine, phenylalanine, threonine, tryptophan, and valine are required by aseptically reared larvae of *C. suppressalis* (63), *H. antiqua* (43), and *P. gossypiella* (106a). Omitting any one of alanine, aspartic acid, cystine, glycine, glutamic acid, hydroxyproline, proline, or tyrosine from the diet of *C. suppressalis* allowed growth similar to that on the complete diet, containing 18 amino acids; but poor growth resulted on diets containing only the 10 essential amino acids as a nitrogen source (63). The relative concentrations of the various amino acids in the chemical diet used for *H. antiqua* seems to be important and optimum levels have yet to be determined (42, 43). Gladstone (47), using *Bacillus anthracis*, showed that studies of amino acid requirements based solely on single deficiencies can be misleading. An amino acid diet recently developed for *P. gossypiella* contains 17 L amino acids and glycine (110).

Various attempts to increase silk production by adding amino acids and other nitrogen compounds to the diets of several species of silkworms have given no unconfounded information concerning their amino acid requirements. This subject has recently been reviewed (55, 73, 79).

Adults of the fruit flies *Dacus dorsalis* Hendel, *D. cucurbitae* Coquillett, and *Ceratitis capitata* (Wiedemann) require amino acids in their diets for high fecundity; honeydew probably constitutes the main source of free amino acids for these flies (52). *Bombyx mori* (Linnaeus) converts phenylalanine to tyrosine (20, 45) as does *C. suppressalis* (65). No determinations of the amino acid requirements of any homopteron have been reported thus far. Recent reviews (73, 112), however, reported studies showing that plant sap apparently contains adequate supplies of free amino acids and amides for aphids;

and since honeydew has been shown to contain considerable quantities of amino acids, its secretion should not now be regarded as a means of bypassing excess carbohydrate and water in order to concentrate nitrogenous compounds.

Lipides

The fat-soluble fraction of most leaves varies between 0.2 and 1.7 per cent but ranges as high as the 7.9 per cent found in sagebrush (78). Seeds and other plant parts often contain much higher concentrations. The fatty acids of leaf, stem, root, and fruit coat are palmitic, oleic, linoleic, and occasionally linolenic acid; the 18 carbon acids in the leaf tend to be more unsaturated than the storage fats in the roots and fruit coat; seed fats contain other fatty acids than those listed above, and the lipides of seeds are characteristic and their chemical composition can be closely associated with the systematic classification of plants (54). Sterols, waxes, carotenes, fat-soluble vitamins, and phospholipides are also present in plants in small amounts.

Fats and fatty acids.—Most insects can utilize dietary fat or fatty acids for energy, for a source of metabolic water, and for building reserves of depot fat and glycogen. The percentage of body fat usually increases as the larva develops and lessens when the insect becomes adult. *Leptinotarsa decemlineata* (Say), however, contains only 3 per cent fat in the larval stage and 13.4 per cent in the adult (102). The body fat of insects is affected quantitatively and qualitatively by their diets. Mature larvae and pupae of *Heliothis zea* (Boddie) [referred to as *H. armigera* (Hübner)] contained more fat when the larvae were reared on high-fat, dough-stage corn than on lower-fat, milk-stage corn; although the iodine and saponification values of the corn lipides at both stages remained almost constant, the fat of larvae fed dough-stage corn was less saturated and had a lower saponification number than that of larvae fed on corn at the milk stage (30). Insects can synthesize depot fats from carbohydrates and proteins. *B. mori*, when ready to pupate, contains about twice as much fat as it has ingested (106). The leafhopper *Circulifer tenellus* can synthesize fat when fed aseptic glucose or fructose (46). Many detailed analyses of the body fats of insects are given by Scoggin & Tauber (93), Timon-David (102), and Hilditch (54). The grasshopper *Schistocerca gregaria* Forskål uses fat as a major source of energy for flight (113).

The only insects that diet studies have shown to require fats or fatty acids are *Pyrausta nubilalis* (9), *Pectinophora gossypiella* (108), *Pseudosarcophaga affinis* (Fallén) (58), *Calliphora vicina* Robineau-Desvoidy (94) [= *C. erythrocephala* (Meigen)] and three species of *Ephestia* (37). Requirements of *Pyrausta nubilalis* can be met with wheat-germ oil, corn oil, or a mixture of cholesterol, linoleic acid, and alpha tocopherol in the diet (9). Omitting fat from the diet of *Pectinophora gossypiella* caused some of the insects to die early in the pupal stage and the remainder failed to emerge; adding corn oil allowed normal development, apparently because of its linoleic acid content (108). Later work showed that 80 mg. of linoleic acid

per 100 gm. of diet permitted normal development (109). Linolenic acid is similar to linoleic in promoting emergence but oleic acid is inactive (106a). Chemical analyses of *Loxostege sticticalis* (Linnaeus) and certain of its host plants suggest that linoleic acid is a dietary essential for larvae of this webworm. Sterile females did not contain fatty acids with more than one double bond (86). Fatty acids are not required by larvae of *H. antiqua* (41) or *C. suppressalis* (60).

Sterols.—All insects studied thus far have required a sterol in their diets and phytophagous species are no exception. This indicates that insects cannot synthesize sterols from acetate as can the rat and other vertebrates. Block *et al.* (18), using *Dermestes maculatus* Degeer [= *D. vulpinus* Fabricius], showed that acetate tagged with C^{14} is incorporated into the triterpenoid hydrocarbon squalene but not into lanosterol or cholesterol. The dietary requirement for sterols in this species is attributed to an interruption of sterol biogenesis at the squalene stage. The biochemical role of sterols in insects is as yet unknown (62). Cholesterol has been used in most chemical diets developed for plant-feeding insects (9, 32, 41, 108) although it is not the characteristic sterol of the higher plants. When the plant sterol ergosterol, sitosterol, or stigmasterol was substituted for cholesterol in the artificial diet for *P. gossypiella*, the larvae grew faster and were larger (108). The weevil *Callosobruchus chinensis* can utilize tetrahydrostigmasterol, which lacks the double bond between C_5 and C_6. Substituting *epi*-cholesterol for cholesterol in the artificial diet slowed the growth rate and produced smaller adults. Isomerization of the OH group at C_3 did not occur (62). Adding cholesterol, sitosterol, or stigmasterol to the ether-insoluble fraction of seeds of *Paseolus vulgaris* allowed development of larvae of this weevil. Tests with 21 sterol analogues showed that the OH group at C_3 is essential and substituting an OH group on C_5 or C_7 blocks utilization; that double bonds at C_5—C_6 and in the side chain are not essential for larval growth and that certain sterol esters capable of being hydrolyzed in the alimentary canal allow growth (59). The structural configuration at the C_3 position is extremely important in determining what cholesterol analogues can be utilized by *Blattella germanica* (Linnaeus) (82). Cholesterol is probably esterified during absorption in this species (81). No one has demonstrated that any insect can utilize calciferol or related compounds with vitamin D activity; the steroid hormones are also not nutritionally effective.

Waxes.—Possibly some phytophagous insects can utilize the waxes found on leaves but it is unlikely that specific compounds are required. The greater wax moth, *Galleria mellonella* (Linnaeus), can be reared on a wax-free diet although it can metabolize waxes and feeds on a diet high in these compounds (53).

Phospholipides.—Lecithin, a phosphoric acid ester of a diglyceride and choline, increases the fecundity of *L. decemlineata*. Females laid an average of one egg per day when fed young potato leaves painted with sucrose solution, three per day when fed leaves painted with a lecithin-sucrose emulsion;

choline offered under the same conditions had no effect (51). Phospholipides are not incorporated into the chemical diets thus far developed for phytophagous insects (9, 41, 62, 107).

Carotenoids and fat-soluble vitamins.—Carotenoids affect coloration of certain insects (49, 71, 80) and the astoxanthin present in the eyes of *Schistocerca* and *Locusta* spp. may affect photoreception (49). In 1953, Fraenkel (38) stated that the carotenes of plants might be important nutritionally because of their conversion to cuticular pigments in certain phytophagous insects but pointed out that no experimental evidence of this was available. Dadd (28) recently showed that omitting β carotene from an artificial diet for *Schistocerca gregaria* Forskål retarded growth, caused high mortality, and affected the development of characteristic yellow and red body colors. Vitamin A acetate allowed as good growth and development as β carotene but no color development, suggesting that the growth-promoting role of carotene is independent of pigment formation. Dadd speculated that a derivative common to both carotene and vitamin A is the actual growth factor (28). Goodwin & Srisukh (48) stated that preformed vitamin A does not occur in this species. Yoshida (118) showed that some carotene or other provitamin A was converted into vitamin A in *B. mori.* Murthy (79) claimed that adding carotene to mulberry leaf powder that had been extracted with benzene was beneficial for *B. mori.* Work with chemical diets showed that carotenes are not required by the species studied thus far (9, 11, 41, 63, 107, 110). No one has yet clearly demonstrated that insects require any of the fat-soluble vitamins D, E, and K, although tocopherol is included in the artificial diets for *Pectinophora gossypiella* (110) and *Pyrausta nubilalis* (11).

Water-Soluble Vitamins

Complete vitamin assays done under aseptic conditions with chemically defined or highly refined artificial diets have been published for only two phytophagous insects namely: the Asiatic rice borer, *C. suppressalis* (60), and the onion maggot, *H. antiqua* (41). The chemical diet developed for *Pyrausta nubilalis* contains choline, thiamine, riboflavin, nicotinic acid, pantothenic acid, pyridoxine, inositol, *para*-aminobenzoic acid, folic acid, and biotin (11); choline is essential (9) but the dietary need for the other vitamins has not yet been determined. The most highly defined diet used successfully with larvae of *Pectinophora gossypiella* differs from that used for the European corn borer in that it contains vitamin B_{12} and lacks inositol and *para*-aminobenzoic acid (110). The indispensable vitamins for *P. gossypiella* are niacin, pantothenic acid, thiamine, riboflavin, pyridoxine, folic acid, and biotin (106a). Hagen (52) reported that of nine B vitamins tested, lack of thiamine, nicotinic acid, folic acid, or choline caused a significant decrease in fecundity of *Dacus dorsalis* adults.

Biotin.—Biotin is required in minute amounts, 0.02 μg. per ml. of diet satisfying the need of *H. antiqua* larvae (41). The small amount needed in

the diet can be supplied by microorganisms, and consequently the dietary need for this vitamin has been determined with antivitamins (60) or with highly purified chemicals under aseptic conditions (41). Lack of biotin caused death of *H. antiqua* before the pupal stage (41). Ishii & Urushibara (60) were unable to assay directly for the biotin requirement of *C. suppressalis* because of biotin contamination in the agar of the diet. When raw egg white containing avidin, a protein that blocks biotin activity, was added to the diet, the larvae died after the fourth instar. These workers consider that biotin is essential for larval growth. Although the rice moth, *Corcyra cephalonica* (Stainton), is not a phytophagous insect as defined in this review, it is noteworthy that biotin is essential for the larvae; biotin-deficient larvae contained less fat and cholesterol and more nitrogen than larvae supplied with this vitamin (91). Oleic and vaccenic acids at certain critical concentrations can partially replace biotin in the diet of this insect (90).

Vitamin B_{12}.—A definite requirement for vitamin B_{12} has not yet been shown for any phytophagous insect. This vitamin is not synthesized by higher plants (55). Adding B_{12} to a synthetic diet used for *H. antiqua* apparently increased larval survival slightly (41). It is used in the pink bollworm diet although its necessity has yet to be determined (107). It is not used in the diet developed for the aseptic rearing of *P. nubilalis* (11). Takahashi (98) analyzed the B_{12} content of silkworms and mulberry leaves; no B_{12} was detected in the leaves but the larvae contained as much as 2 mg. per 100 gm. of fresh weight. These findings were confirmed by Sahashi *et al.* (89). The work was not done aseptically and more recent work of Takahashi (99) indicated that the B_{12} was formed by actinomycetes in the alimentary tract. Adding B_{12} to fresh mulberry leaves increased silk production in *B. mori* (79).

Thiamine.—All insects studied critically to date have needed thiamine supplied either directly in the food or by microorganisms in the gut. Attempts to grow *C. suppressalis* larvae on thiamine-free artificial diets containing one or both of the pyrimidine and thiozol derivatives of this vitamin failed; when either or both 2-methyl-4-amino-5-bromomethyl-pyrimidine HBr or 4-methyl-5-B-hydroxyethyl thiozol were added instead of thiamine, all the larvae died before the fourth instar (60).

Riboflavin.—The malpighian tubules of most insects contain high concentrations of this vitamin, in some insects more than 30 times the concentration found in beef liver (31, 75). It occurs in two forms, free and in a bound cytoplasmic storage form. Drilhon & Busnel (31) surveyed 13 species and found the highest riboflavin content in the malpighian tubules of phytophagous insects. The riboflavin content in pupae of *Sphinx lugustri* Linnaeus increased during development from 500 to 5000 μg. per gm. of fresh malpighian tube tissue (31), and Hinton (55) reports findings that suggest that certain insects produce riboflavin by biosynthesis. This view is supported by Kikkawa (71). There is apparently a close metabolic link between riboflavin and the formation of uric acid (71). The entire riboflavin content

of the egg of the grasshopper *Melanoplus differentialis* (Thomas) is converted into pterins during development; this conversion is a function of the developing embryo and stops in eggs in which the embryo is killed by x-radiation (19). Most insects require a dietary source of this vitamin for normal development. All aseptic larvae of *H. antiqua* on a riboflavin-free chemical diet died before the third instar and some died within two days after hatching (41). Larvae of *C. suppressalis* survived an assay period of 30 days under aseptic conditions on a riboflavin-free synthetic diet but their growth rate was greatly retarded (60).

Pyridoxine.—Lack of pyridoxine slowed the growth rate of aseptic larvae of *H. antiqua* and caused 100 per cent mortality before the third instar (41). No larvae of *Chilo suppressalis* lived past the second instar when reared aseptically on a pyridoxine-free diet (60). It is notable that *Pseudosarcophaga affinis*, a parasite of the spruce budworm, does not require this vitamin (57). Studies with the stored product insect *Corcyra cephalonica* provided information concerning the metabolic role of this vitamin in insects. Larvae of *C. cephalonica* fed a pyridoxine-deficient diet high in DL tryptophan or DL kynurenine excreted yellow faeces containing kynurenine and 3-hydroxy-kynurenine, indicating a block in tryptophan conversion at the 3-hydroxy-kynurenine to 3-hydroxy-anthranilic acid stage (97).

Nicotinic acid.—Only 9 per cent of larvae of *C. suppressalis* survived a 30-day assay period on a synthetic diet, lacking nicotinic acid, the larvae growing much slower than normal; feeding pyridine-3-sulfonic acid, which is antagonistic to nicotinic acid in the bacterium *Proteus vulgaris*, did not block nicotinic acid utilization in larvae of this insect (60). When this vitamin was omitted from the diet of *H. antiqua*, all the larvae reached the second instar but then 97 per cent of them died (41). Whether *B. mori* can convert tryptophan to nicotinic acid via the reaction sequence tryptophan→kynurenine→3-hydroxy-kynurenine→3-hydroxy-anthranilic acid→nicotinic acid is controversial. Kikkawa (71) considers that most of the nicotinic acid in this silkworm comes from the mulberry leaves it eats and that it cannot convert tryptophan or tryptophan metabolites to nicotinic acid. Injecting tryptophan, 3-hydroxy-kynurenine, or 3-hydroxy-anthranilic acid into *B. mori* pupae failed to increase pupal nicotinic acid (71). These results agree with those of Ito (66), but Kato & Hamamura (67) claimed that nicotinic acid and niacinamide increase during pupal metamorphosis although they did not identify tryptophan as the precursor. A great amount of nicotinic acid is excreted by *B. mori* at the time of emergence from the pupal case (66). Niacinamide is deaminated and not methylated, as it is in certain carnivorous mammals, before excretion by larvae of *B. mori* and *Lucilia caesar* Linnaeus (68).

Choline.—Choline is essential for many insects and much more of it is required than of some other water-soluble vitamins. It is present in most plant tissues (116). Omitting choline from the diet used to rear aseptic larvae of *Pectinophora gossypiella* prevented development beyond the third

instar (108). Choline had to be added to yeast extract in the artificial diets developed for *Pyrausta nubilalis* (9) and the southern armyworm, *Prodenia eridania* (32). When choline was omitted from an artificial diet on which *C. suppressalis* was reared aseptically, all the larvae in one replicate died in the first instar but 81 per cent of those on three identical replicates survived the 30-day assay period at a greatly reduced rate of growth; the authors did not definitely conclude that this vitamin is essential (60). Lack of choline prevented aseptically reared larvae of *H. antiqua* from pupating although 79 per cent of them reached the third instar; growth from hatching to the third instar was only slightly slower than that of larvae reared on a complete diet (41).

Folic acid.—Lack of folic acid prevented *H. antiqua* larvae from forming normal pupae (41). All aseptic *C. suppressalis* larvae on folic acid-free diets died before the third instar (60). Folic acid is necessary for most insects that have been studied critically, although it is not essential for *Pseudosarcophaga affinis* (57).

Pantothenic acid.—As a constituent of coenzyme A, pantothenic acid is involved in the acetylation of cholesterol, fatty acids, choline, and amino acids. It has been shown to be essential for all insects studied critically. In some insects it is supplied by intracellular microorganisms (73). Lack of this vitamin slowed the growth of aseptic larvae of *C. suppressalis* and caused 96 per cent mortality, mostly in the third instar, during a 30-day assay period (60). On a diet lacking pantothenic acid but containing 1.5 μg. (217×10^{-6} Lipman units) of coenzyme A per ml., all the larvae of *H. antiqua* died before pupation, the deficiency not being apparent until the second instar. Probably the pantothenic acid requirement was partially fulfilled by the small amount of coenzyme A in the diet. Diets lacking coenzyme A but containing 6 μg. of calcium pantothenate per ml. of diet allowed normal development (41).

Para-aminobenzoic acid.—This vitamin is a structural part of folic acid and is essential for the growth of certain microorganisms (74). It is not required by larvae of *C. suppressalis* (60) or *H. antiqua* (41). It is used in artificial diets for *Pectinophora gossypiella* (107) and *Pyrausta nubilalis* (9) although its essentiality has yet to be determined with these species.

Carnitine or vitamin B_T.—Carnitine (B-OH-butyrobetaine) is required by certain tenebrionid beetles but need for it has not been demonstrated for any phytophagous species. The nutritional role and biochemical activity of this compound were recently reviewed (55, 72, 73).

Inositol.—Inositol occurs in plants as a structural part of phytin, an organic phosphorous compound (74). It is not required by any phytophagous insect studied to date. It is used in the synthetic diet developed for *P. nubilalis* (11) although its essentiality has yet to be determined for this species.

Ascorbic acid.—Omitting ascorbic acid from a semisynthetic diet slowed growth and caused death of nymphs of *Schistocerca gregaria* in the fourth

instar (28). Adding ascorbic acid to benzene-extracted mulberry leaf powder increased survival of *B. mori* larvae (79). Thorsteinson (101) showed that ascorbic acid induces feeding in *Plutella maculipennis* (Curtis), *Chorthippus longicornis* Latrielle, and *Leptinotarsa decemlineata* under artificial conditions. Perhaps the beneficial effects of this vitamin reported above (28, 79) were due in part to phagostimulation since it is generally considered that most insects synthesize this vitamin (55).

Special factors.—P. nubilalis requires a dietary source of one or more unidentified factors known as "the corn leaf factor," which occurs in corn leaves, grass juice, and certain other plant materials (11). It is heat- and acid-stable, water-soluble, and dializable and is not identical with any of the known B vitamins, ascorbic acid, sodium nucleate, citrovorum factor, or carnitine. A study of the feeding reactions of first-instar larvae demonstrated that this factor is not a required feeding stimulant (12). Females require a higher level of corn leaf factor than males; deficiency symptoms include failure to escape from the pupal case, failure of wings to expand, and occurrence of death within one or two days after emergence (11).

Larvae of *C. suppressalis* grew faster when a water extract of yeast was added to 10 B vitamins in an artificial diet; but even on diets containing dry yeast and rice-stalk meal it was difficult to obtain perfect females, many being unable to emerge from the cocoon (60). Further work with this species suggested that there is an unknown factor or factors in the rice plant that affect emergence from the pupal case; whether it is identical to the corn leaf factor is uncertain (64).

Adding cotton-leaf meal or dried forage-plant juice to diets did not increase the growth rate of larvae of *P. gossypiella*, nor did adding these make the medium more attractive to the larvae (107).

Larvae of the onion maggot complete normal development on diets completely free of plant extracts (41).

Minerals

No one has yet determined the exact mineral requirements of a phytophagous insect. Various salt mixtures developed for vertebrate diets have been used in the artificial diets tested thus far (9, 32, 41, 108). Since insects do not need calcium for bone formation, these mixtures probably contain much more calcium than necessary. The reviews of Trager (104) and Levinson (72) contain sections on the mineral requirements of insects. In 1956, Lipke & Fraenkel (73) reviewed the effect of soil fertility on the nutrition of phytophagous insects; there have since been no outstanding developments in this field. Uvarov (106) gave an extensive review of the older literature on the mineral composition of insects. The zinc content of reproductive tissues of *B. mori* is high and this mineral is probably important for reproduction in this species (1).

The little that is known about the mineral requirements of phytophagous insects is largely based on a series of experiments measuring the growth or

reproductive capacity of insects fed on plants deficient in various minerals (3, 4, 7, 8, 26, 87, 88, 96). The results of these experiments should not be interpreted solely in terms of the mineral deficiencies of the test plants. Plants deficient in minerals are abnormal and may contain atypical concentrations of organic compounds (77) that can affect the growth or reproductive capacity of the insects feeding on them (88). The insect reacts to the chemicals present in the tissues upon which it feeds, but the chemical composition of the tissue depends upon the physiological condition of the plant and the mineral deficiency is so confounded with the over-all condition that specific deficiency effects upon the insect cannot be measured.

Nitrogen fixation.—There has been considerable controversy as to whether termites and aphids can utilize atmospheric nitrogen, either directly or through nitrogen-fixing microorganisms. The subject was fully reviewed recently (73, 104), and as yet there is no clear-cut record of nitrogen fixation on a scale that would significantly affect the protein economy of these insects.

Other Factors

Water.—Phytophagous insects normally feed on a diet with a high water content. Numerous writers have observed that feeding on wilted foliage produces adverse effects (70, 79, 95, 100). These effects may not result merely from a decrease in the supply of dietary water since many concomitant chemical changes occur during wilting (14). A supplementary water supply was necessary when *Oncopeltus fasciatus* (Dallas) and *Euschistus variolarius* (Palisot de Beauvais) were fed on a dry synthetic diet (92). The specific gravity of the haemolymph of larvae of *Neodiprion lecontei* (Fitch) fed wilted, cut foliage was significantly higher than that of larvae fed on the growing foliage of pine trees (6). The chemical diets developed so far for phytophagous insects contain 76 to 89 per cent moisture (63, 108). Although no direct studies have been conducted on their water requirements, phytophagous insects appear to require a high water intake for normal development.

Nucleic acids, purines, pyrimidines.—Ribose nucleic acid, thymine, and inosine are included in the chemical diet developed for *H. antiqua* (41) although their dietary necessity has not yet been determined. None of these compounds is used in the various diets developed for *C. suppressalis* (63) or in the diet for *Pyrausta nubilalis* (11). Adding ribose nucleic acid to a chemical diet had no stimulatory effect on *Pectinophora gossypiella* (107).

Chlorophyll.—No one has yet demonstrated that chlorophyll is an essential nutrient for a phytophagous insect. It is apparently utilized by *B. mori* (24, 118). Studies of its metabolism in *Anasa tristis* (DeGeer) have shown that it is broken down in the gut wall (76). The porphyrin ring is apparently opened during digestion by *B. mori* and pyrrole or indol derivatives are absorbed. Yoshida therefore claimed that the chlorophylls have no specific physiological activity in this species, being broken down during digestion and absorption (118).

Nutritional Requirements and Host Specificity

In 1956 Lipke & Fraenkel (73) reviewed the many papers on host preference in phytophagous insects. They stated that the most fundamental aspect of this problem is whether selection is governed "(a) by the nutritional superiority of the plants or region of the plant serving as food for the insect or (*b*) by the presence or absence of attractants and repellants in plants of more or less uniform food value to which the parasitic insect has become adapted." They then presented the available data, which suggest that the gratification of nutritional requirements plays a minor role in the insect's choice of a suitable host plant. However, very few determinations of the qualitative nutritional requirements of phytophagous insects are available and no quantitative studies have been reported. Until more information is available, speculations as to the relative importance of nutritional requirements and attractants and repellants in governing host selection must be regarded as highly theoretical. In his 1953 review of the role of nutritional factors in host plant selection, Painter (84) stressed the lack of adequate data to support interpretations in this field of biology.

Beck (14) states that many experiments measuring the effects of feeding various host plants to phytophagous insects have been conducted and that though striking differences in host plant suitability have been demonstrated, the role that the nutrient content of these plants played in the experimental results has not been determined.

Previously, Fraenkel (38) advanced the view that the nutritional requirements of all insects are "essentially similar" and that the host range of a phytophagous species is consequently determined by its reaction to chemicals and conditions that satisfy its chemical and physical feeding requirements. This stand was questioned by Beck (14), who pointed out that the dietary requirements of the insects studied thus far differ in a few significant particulars and that there may be differences in the qualitative and quantitative requirements that are important in determining an insect's range of host plants. Beck also showed that sugar and protein levels can play a role in the feeding reactions of larvae of *P. nubilalis;* these borers require a low sugar-high protein diet early in larval life and a high sugar-low protein diet for the later instars; these requirements are met by the insect moving from low sugar-high protein leaves to plant tissues with a higher sugar ratio during the late-second or early-third instar (12, 14, 15). Thorsteinson (101) has recently showed that ascorbic acid, thiamine, sucrose, glucose, betaine, and monosodium glutamate stimulate feeding in grasshoppers but asparagine and glycine have no effect within a range of 0.5 to 0.0008 *M*. He considered that there is little basis for differentiating between an insect's perception of chemical feeding factors and certain nutrients since it responds to both chemotactically.

In past years entomologists have thought that an insect's behavior is directly determined by its nutritional needs. Kennedy (69) considers that the reaction against this old belief has gone too far and is now an obstacle to

progress. He states "The main point here is that both kinds of stimuli [those activated by chemical feeding factors and by nutrients] are provided by the same plant, the same leaf. We shall be able to separate them only experimentally, when we have a good artificial feeding technique. Both kinds of discrimination operate in every act of selection, so that plant-physiological preferences [activated by stimulation provided by nutrients] can determine selection even between kinds of plants." Although Kennedy's paper specifically discusses host selection in aphids, the writer considers this a most useful concept for many phytophagous insects.

No direct evidence of plant resistance to insect attack because of specific nutritional deficiencies or harmful imbalances of nutrients is available though Auclair & Maltais (5) showed that juice from a pea resistant to aphid attack contains a lower concentration of amino acids than juice from a susceptible variety. Beck (17) claims that the saccharotrophic behavior of first-instar larvae of *P. nubilalis* would cause them to feed on plant tissues with the lowest concentration of certain toxic substances, and consequently sugars may have played a significant role in the adaptation of *P. nubilalis* to the corn plant. The few correlations between resistance and nutrients in Painter's review of insect resistance in crop plants (83) emphasizes how little is known.

Phytophagous insects eat to satisfy their requirements for essential nutrients and in so doing destroy enormous amounts of food and fiber. As Trager (104) aptly stated, "What an insect eats and how much it eats largely determine it ecological role and its economic importance." Obviously a better understanding of the link between phytophagous insects and their host plants is severely hampered by the lack of information on the nutritional requirements of this economically important group.

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RECENT ADVANCES IN SILKWORM NUTRITION[1]

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This review is limited to the most recent papers concerned with the nutrition of the silkworm, *Bombyx mori* (Linnaeus). This field, together with that of genetics, is currently considered the major area of research in sericulture, for, from the scientific point of view, the silk production of the world depends on them. Several problems in relation to silkworm nutrition have become important through attempts to develop an artificial or semi-artificial method of feeding that would make possible the industrialization of silkworm raising.

INGESTION

Quantitative Aspect

Chang (15) confirms the result given by Itaya (39), that ingestion in the silkworm does not depend on a nycthemeral rhythm. It is sensitive, on the contrary, to several other factors [Legay (54)]. Previous starvation stimulates food consumption, providing that this starvation does not exceed 36 hr., after which the effect is the reverse. The age of the larva affects the consumption index, which undergoes cycles at each intermolt (at a maximum in the middle of the intermolt) and which, moreover, decreases from birth to maturity. Ingestion by the female is greater than that by the male, but the index is the same. The effect of temperature change is complex and varies, depending on whether it acts for a long or a short period of time; moreover, individual responses differ markedly.

Study of the mode of distribution of the food has led to the conclusion that the silkworm feeds continuously. Actually, however, it makes a series of small feedings, and the ingested quantities vary a great deal during a 24-hr. period (Figure 1 shows possible cycles during 8 hr.). Excretion goes on regularly.

The quality of the mulberry leaf has a great influence on the amount ingested. Not only the physico-chemical characteristics in relation to the age of the leaf [Fraisse (27)], but also the characteristics of the mulberry varieties, affect the amount ingested, so that a qualitative underfeeding is always linked with a quantitative underfeeding [Legay (54)]. This explains why it is possible to obtain a supernumerary molt either by feeding on autumn leaves or by a quantitative underfeeding.

The importance of the various above-mentioned factors is not equal;

[1] The survey of the literature pertaining to this review was completed in June, 1957.

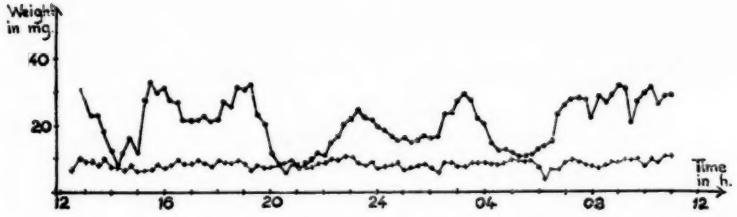

FIG. 1. Variations of ingestion (above) and excretion (below) in the silkworm with time (measured every 15 min. during 24 hr.).

when many of them are working at the same time, a hierarchy is created and one of them becomes dominant.

QUALITATIVE ASPECT

That the silkworm feeds primarily on mulberry leaves is one of the chief reasons for the economic difficulties of sericulture, since this limits silkworm raising in time and place and prevents real industrialization. Therefore, this problem has been attacked for years by many workers in very different ways.

Research on attractant substances determining the feeding.—No definite conclusion based on this research is yet possible. Several experiments prove that there are attractant substances, quite stable and especially resistant to heat, and nonspecific to the mulberry tree. They exist in several plants, which have in common the presence of latex. According to Hamamura (36), the substances responsible appear to be glucosides. Their isolation would be of major importance.

Research on succedanea.—Several plants can be added to the list of the known succedanea, or substitutes, for the mulberry leaves: *Xylosma raremosum* [Lahargue (50)], the fruits of *Ficus carica* [Bounhiol (12)], and especially *Podospermum laciniatum* [Pascal (69)], which gives results very close to those obtained with *Scorzonera hispanica*. With the appropriate techniques, one obtains a full development of the silkworm on *P. laciniatum*, as well as on *S. hispanica;* it is possible to raise several successive generations on both of them; therefore, selection is possible. In the near future, the leaves of *Scorzonera* may be used in the northern countries instead of mulberry leaves, in the event of the temporary depletion of the latter [Wasowicz (80); Fedorov (24)].

Research on preserved mulberry leaves.—Numerous processes have been tried, including a moderate refrigeration (+3° C.). This method gives good results but cannot be continued for a long time because of the development of fungi, which is difficult to prevent permanently. It is also interesting to note that the silkworm accepts cooked mulberry leaves [Legay & Pascal (58)]; food preserved by means of "pasteurization" is therefore possible.

Nevertheless, such leaves do not permit normal and complete development, and little by little the appetite decreases and growth slackens. These symptoms imply a vitamin deficiency, but this problem has not been experimentally elucidated.

Research on silkworms with modified olfactory sense.—Another way of resolving the problem is to obtain silkworms which do not show the usual alimentary specificity. Torii & Morii (76) pointed out that the origin of attraction of the silkworm to mulberry is located in the antennae as far as distance attraction (3 cm.) is concerned, and on the maxillae as far as contact is concerned. Following this work, Tazima (73, 74) obtained, after x-ray irradiation, mutants whose olfactory organs of the maxillae are probably degenerated, or deeply modified. Silkworms of this type accept any food; but the problem of nutritional requirements is not yet solved. The mutant silkworms fed on beetroot leaves do not develop very well; they make their cocoons and metamorphose only if they are given mulberry leaves during the last days of their larval life. Therefore, for the *B. mori* races, at the present state of silkworm selection, only the mulberry tree appears to contain the suitable quantity and quality of nutritive elements necessary for the complete development of the animal.

NUTRITION

Many analyses have already been made of the silkworm and its food, the mulberry leaves. In this general field, two developments are noticeable:

The first consists of the accumulation of data making it possible to compare, at a given moment, the composition of the silkworm and that of the leaves. Recent information has been given by Comenge (16, 17) concerning inorganic and organic substances, and by Fukuda (29) concerning the amino acids. The second consists of following the variation of composition with the age of the silkworm [Comenge (16)] or with the age of the leaf [Demianovski & Doman (23); Makarevskaya (61); Fraisse & Laudanski (27)]. We shall specify only some important points.

Vitamins

Vitamin A.—Franceschini (25) noted the effect of vitamin A (1 I.U. per gm. in a white-silk race and from 12 to 14 I.U. per gm. in a yellow-silk race) on silkworm eggs and tissues. Moreover, there was 1.7 mg. β-carotene per kg. in fresh mulberry leaves. Yoshida (83) showed evidence that the carotenoids of the leaves are decomposed by enzymatic action in the digestive tube into carotene and xanthophylles; the provitamin A so formed is changed into vitamin A in the blood. The author adds that the role of this vitamin is certainly not as important in the silkworm as in the vertebrates.

Vitamin C.—Caro & Rovida (14) found that the mulberry leaf can be classified among the plants which are richest in vitamin C. It has a vitamin C content of 1.3 mg. per gm. (biological dosage) to 1.8 mg. per gm. (chemical dosage). They notice especially that the silk gland itself is very rich in

vitamin C (0.7 mg. per gm. at the fourth instar). In fact, the variations of this content are cyclic with each larval stage (minimum during the molts); moreover, there is an increase from the egg (0.12 mg. per gm.) and the young larva (0.3 to 0.4 mg. per gm.) to the fifth instar (0.7 mg. per gm.). The study of the variations in ascorbic acid according to the development of the silkworm was undertaken again by Gamo (31), while the ingested quantities retained and used for the growth of the different organs have been measured [Gamo *et al.* (32)]. Moreover, it is interesting to note that vitamin C is synthesized, during the pupal stage, in the fat tissue as a result of the dehydrogenation of mannose. This transformation was obtained *in vitro* [Gamo & Seki (34)]. Finally, the role of vitamin C was verified by adding it to leaves which had previously been made deficient by shading or heating them [Gamo & Nishiyama (33)].

Vitamin B_2.—Kishi (47) noted that spraying silkworm larvae and pupae with vitamin B_2, in aqueous solution, increases the percentage of protein in the insect, while the fat content decreases or remains the same. Kirimura (46) determined the content of B-group vitamins in mulberry leaves and its variations according to a series of natural factors.

Vitamin B_{12}.—The vitamin B_{12} content in *B. mori* changes according to the stage of development. It is maximum in the larvae, minimum in the eggs, and, in the organs, is greatest in the Malpighian tubes [Takahashi (72)]. Synthesis of cobalamine could be realized through the Actinomyces in the digestive tube. Supplementation of mulberry leaves with vitamin B_{12} increases the protide content of the larva but not the silk production [Bosticco & Arnaudo (8)].

Vitamin PP.—It appears likely that, except for a small quantity synthesized by the intestinal flora, the greater part of the required nicotinic acid is obtained by the silkworm from the mulberry leaf, as is the case with tryptophan. Experiments in which possible precursors of nicotinic acid (i.e., tryptophan, 3-hydroxykynurenine, 3-hydroxyanthranilic acid) are injected into the silkworm have led only to negative results. Even a study of the "White 1" strain which lost the ability to transform tryptophan into 3-hydroxykynurenine has yielded no positive results [Kikkawa (44); Kikkawa & Kuwana (45)]. However, other authors have observed contrary results [Kato (42, 43); see also Hinton (37)].

If normal mulberry leaves are supplemented with nicotamid, there is no "proterogynous" effect on the occurrence of the molts [Bounhiol (9)]. such as Lwoff & Nicolle (60) observed on *Triatoma infestans* Klug. On the contary, Bounhiol has observed that strong doses given to young silkworms cause loss of appetite and failure to develop normally.

Inorganic Constituents—Trace Elements

Bone (7) has noticed the rather important fact that there is an abundance of potassium as compared with sodium in phytophagous insects, while the opposite situation is characteristic among carnivorous insects. Tobias

(75) points out that the silkworm's haemolymph presents a ratio Na/K = 0.35, and that the pupa contains practically no sodium [see the discussion by Buck in Roeder (13)]. The little sodium existing during the larval life must come from a simple equilibrium of diffusion with the sodium of the food. The mechanism of sodium exclusion before metamorphosis and its meaning are not yet known. However, recent experiments with the injection of salts [Yoshitake (84)] allow the supposition that potassium has an influence on determining the voltinism and that it directly affects the egg-cells in the process of development. Furthermore, it is now known that, in a general way, sodium and potassium ions act on protein synthesis [Allfrey *et al.* (2)].

A systematic study by Comenge & Guelbenzo (21, 22) on minerals, including 18 elements, indicates that three of them (silver, copper, and titanium) play a prominent part and can be considered as oligo-elements. Fukuda & Matuda (30) have carried on more detailed analyses taking into consideration the tissues. Besides these analytical researches, the synthetic ones by Gamo & Nishiyama (33), who supplemented previously injured mulberry leaves, showed the efficiency of magnesium phosphate, $Mg(H_2PO_4)_2$, on the growth and health of the treated silkworms (35).

DIGESTION AND ASSIMILATION

Rate of Passage of Foodstuffs

Legay (54) confirmed by the radiographic method that the time required for food to pass through the alimentary tract of the silkworm was from 2 to 3 hr. This is the minimum time, for part of the food may be retained longer than the rest, and, moreover, there are noticeable variations according to age and health.

Digestibility

The coefficient of digestive utilization (C.D.U.) and the ratio of gain weight to food retained weight (R. W.), as we have defined them [Legay (54)], are very much affected by the food quality. They may be estimated in fresh or in dry weight:

	Fresh Weight			Dry Weight
Rearing season	April	May	July	May
C.D.U.	0.62	0.58	0.43	0.30 to 0.35
R.W.	0.87	0.80	0.58	0.60

For silkworms in the fourth instar, the water metabolism is such that the larva keeps its water content at 88 per cent, ingesting leaves containing 70 per cent water and passing excreta containing 50 per cent water. But the percentages of retained and eliminated water vary according to the age of

the insect [Comenge (17)]. This variation, however, is partially caused by the water content of the mulberry leaf itself. Trager (77) established a comparison between the digestibility of nutrients in the silkworm and that in the cow from the old data of Hiratsuka and Maynard.

Recently, Maymone (64) also undertook research in comparative physiology concerning the digestibility of the mulberry leaves in the silkworm and in a vertebrate, the sheep. This work gives us interesting data on the digestibility of the organic elements in *B. mori* (Table I).

TABLE I

ASSIMILATION OF FOOD ELEMENTS BY SILKWORMS ACCORDING TO RACE AND INSTAR (IN PER CENT)

Race	Larval stage	Organic Compounds	Pure Protides	Crude Fat	Crude Fiber	Nitrogen free extract	Lignin
"Japonais vert"	4th	84.7	93.1	97.5	68.1	83.8	77.0
	5th	46.5	83.6	80.0	—	36.1	28.4
"Blanc novi"	4th	73.8	89.0	95.5	48.6	71.8	58.0
	5th	58.5	86.8	84.9	24.2	51.8	30.5

It may be noticed that these results, following those of Comenge (18) confirm at least the partial digestion of cellulose; this fact has not yet been explained. Moreover, the important differences between these figures and Kellner's old data (64) may arise not only from a change in techniques but also from the genetic evolution of the silkworm under the influence of selection. It is not to be forgotten that, within half a century, some races have doubled their weight and with equal weight have doubled their silk yield; in other words, their metabolism has been modified to a large extent.

DIGESTIVE ENZYMES

The intestinal reaction (pH 9 to 10) in the silkworm is more alkaline than in most other insect larvae [Waterhouse (81)]. This could explain the degree of sterility of the gut of the silkworm.

The last research work on the digestive enzyme followed Matsumura's discovery of two types of amylase in the silkworm. An attempt was made to define the genetic control of amylase activity in the intestinal juice [Matsumura (63)], and in the haemolymph [Kikkawa (44)]. The two amylase types appear to belong to the α-amylase group and to differ only in the quantity of protein content of the enzyme and not in its quality [Seki (70)].

Horie (38) found that the activity of the alkaline phosphatase, which is

concentrated in the striated border of the midgut, changes during the silkworm's development and reaches a peak at the middle of the fifth instar. The effect of starvation on the phosphatase activity is scarcely seen for 24 hr., but thereafter the activity noticeably decreases. It is interesting to note that this result is parallel with our data concerning the influence of starvation on the feeding.

Yamaguchi (82) studied the functional localization of the digestive system and found that the activity of certain enzymes (protease, amylase, and saccharase) both in the gut epithelium and the gastric juice is always remarkably high, especially in the posterior midgut; this fact seems to play an important role in intermediary metabolism, as well as in the digestion and absorption of nutrients.

Pigment Absorption

Pigment absorption changes according to the sex [Yoshida (83)], for example:

	Chlorophylls	Carotenoids
Females	41 per cent	29 per cent
Males	46 per cent	34 per cent

In all probability, it also changes according to the age of the silkworm. The chlorophyll compound is assimilated during the first two instars and during the last one, but not during the third and fourth [Comenge (16)]. When these compounds are assimilated, they are entirely metabolized and decomposed into pheophorbids in the digestive tube, then into pyrolic or indolic derivatives in the blood and the various tissues (in vertebrates the porphyric ring is not broken) (83).

The silkworm's absorption of the carotenoids contained in the mulberry leaves led the way to a series of investigations of both theoretical and practical interest, because the color of the cocoons depends on this absorption. Three chief genes control the cellular permeability of these pigments, at two successive places, the midgut and the silk gland [Jucci (41)]. The observed phenomena suggest three explanations: (*a*) the tissues considered do not absorb the carotenoids; (*b*) they store them, thus preventing them from getting through; or (*c*) they transform them (into a leuco-derivative, for example).

Auxines

Berrier (5) found that the larva contains auxines, which is not surprising, but the reappearance of these elements in the pupa leads to the supposition that an endogenous origin is not impossible.

Absorption of the Phosphorus Compounds

Recent experiments with radioisotopes show that the posterior intestine is the most active in absorbing the phosphorus compounds [Kogure (48, 49); Ito (40)].

Metabolism

The quantity of glucide assimilated by the larva is always very important. The silkworm utilizes most of it but retains a very little which it uses for the synthesis of other products (fats, protides).

It is important to note that from the time of the fourth larval instar there is a synthesis of fats which is particularly active during the fifth instar and results in a storage of these substances. The glucides are the energy foods of the larva, while the stored lipides will be those of the pupa and the moth (that is to say, they will be used during those stages in which there is no feeding) (18).

Protides are always assimilated in great quantities during the fourth and especially during the fifth instar, and their metabolism is very high; but the most striking fact is the synthesis of protides at the time of the third molt (19, 20).

The comparison of all known data tends to confirm the assumption that there are two distinct phases in the life of the silkworm: on the one hand, there are the first three instars; on the other hand, the two last instars [Morohoshi (65); Legay (54); and Allegret (1)]. During the third molt, the discontinuity is marked by a synthesis of protides, and the second phase is characterized by a lipide storage and a decrease in the importance of the glucides.

Intestinal Flora and Effect of Antibiotics

The intestinal content of the silkworm is remarkable because of its lack of microflora. Masera (62) observed that 43 per cent of the larvae he examined have a sterile intestine and that in 57 per cent there can be found only a few species of bacteria and fungi, but these occur in limited numbers. Masera attributes this limited microflora to the antibiotic activity of the intestinal juice, which, in turn, is caused by an unidentified substance, while Itaya (39) attributes it to the strong alkalinity of the gut.

In any case, in a healthy silkworm, such a limited microflora is certainly not able to play a prominent part in the alimentary physiology, although Takahashi (72) admits the role of certain actinomycetes in the synthesis of vitamin B_{12} by the silkworm. For this reason the study of the effect of various antibiotics on silkworm growth and nutrition has incited considerable interest, and a stimulation of the general metabolism is suggested [Murthy *et al.* (67, 68)]. In fact, Bheemeswar & Sreenivasaya (6) presented evidence in the hemolymph, intestine, and silk gland, of a transaminase which produces the following reaction:

$$\text{L-aspartic acid} + \alpha\text{-Ketoglutaric acid} \rightleftarrows \text{oxal acetic acid} + \text{L-glutamic acid}$$

By measuring the glutamic acid produced, Shyamala & Bhat (71) tested the activity of this enzyme in silkworms which had ingested antibiotics, and in control silkworms. An increase of about 35 per cent in the intestine and 8 per cent in the silk gland gave proof of the effect of these antibiotics on the general metabolism.

PHYSIOLOGICAL EFFECTS OF ALIMENTATION

Effects on Growth

The effects of quantitative modifications in alimentation have been well studied. Systematic underfeeding (i.e., suboptimal feedings) of each instar permits definition of the periods of compulsory and facultative feeding [Bounhiol (10)] and the study of their relationship with the determination of the molts (52). Techniques of underfeeding (continuous, discontinuous, repeated at each intermolt) permit an analysis of the relationship between alimentation and growth (obtaining an extra molt, or suppressing one of the molts, or obtaining dwarf adults able to reproduce).

The general idea of these experiments is that the level of activity of one organ in the silkworm (and perhaps in all insects) is always maximum; it is possible to lower it but not to raise it. This physiological phenomenon is one in which vertebrates and invertebrates differ.

We do not know, for the time being, how to overfeed the silkworm quantitatively; nor have the various tests of qualitative supplementation on normal mulberry leaves been positive as to what concerns the total growth. However, Murthy (66) noted an increase of the growth ratio and silk production with mulberry leaves perfused by ammonium nitrate. Ushioda (79) obtained results also with urea-sprayed leaves. Raising on unusual food such as substitutes (*Lactuca*, *Scorzonera*, *Podospermum*), as well as on parts of the mulberry tree other than leaves (stem, stalk, mulberry), leads to important modifications which are possible to analyze [Legay, Pascal & Baud (59); Bounhiol (11)].

Effects on Silk Production

The growth of the silk glands and their secretory intensity are more important in the fifth instar, and they are out of harmony with the rest of the larval life [Legay (51)]. Therefore, a premature cessation of feeding before maturity affects the silk production; the techniques of absolute starvation permit one to follow the development of this secretion [Legay (53)]. However, the direct measurement of nitrogen [Allegret (1)] leads to nearly the same results.

Qualitative changes in the food (autumn mulberry leaves or substitute leaves) bring about significant differences in the quantity of the produced silk [Bergmann (4); Fraisse (26); Trevisan (78)]. Gamo (31) also observed that the variation decreased when the food consisted of mulberry leaves injured experimentally.

Fukuda (28) studied more especially the action of sugars on the development of the silk glands, and he observed that the total nitrogen retention rate in the silk gland rises from 2 per cent in the case of "shaded" leaves to 4 per cent in the case of glucose-coated leaves.

Effects on Egg Production

Fertility and fecundity are very sensitive to quantitative [Legay (57); Baud (3)] and qualitative [Legay (55)] changes in the food. The nitrogen

content of the eggs as related to their number is also modified [Allegret (1)]. It is noticeable that the relative fecundity of silkworms reared in autumn is higher. The repartition of protides effectuated by the animal is different and seems to be in relation to the ratio of glucides to protides in the food; this ratio is higher in autumn than in spring.

Effects on the Characteristics of Descendants

The nutrition of the larva affects the development of the genital rudiments in the larval stage [Legay (55)]. Ovogenesis is affected to the extent that it not only modifies the weight or total number of eggs laid, but also the weight of the individual egg (Baud (3)]. It has been made possible, by nutritional treatment, to obtain embyronated eggs in diapause, weighing from 0.50 mg. to 1.10 mg., while the normal weight of one egg is about 0.7 mg. Such variations affect the development of the larvae which hatch from these eggs, but these variations cease when the food distribution is again normal [Legay (56)].

CONCLUSIONS

This review of the latest work in the field of silkworm nutrition shows that most of the research concerned is carried on to develop a suitable artificial feeding method for the silkworm.

Several problems, dealing with different fields, then occur:

(*a*) *Behavior.*—It is necessary that the silkworm should accept the new food.

(*b*) *Nutrition.*—This food must contain all the elements necessary for the development of the silkworm, especially for its metamorphosis.

(*c*) *General physiology and genetics.*—The effect of this new food should not adversely affect either the silk secretion or reproduction.

We should like to point out that all these investigations, proceeding from practical necessity, are also of great theoretical interest.

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USES OF SOUNDS BY INSECTS[1]

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Use of sounds by insects implies that insects produce special sounds, receive these sounds through sense-organs, and react to them with appropriate behavior patterns. That insects produce sounds has been known since antiquity. Only a hundred years ago, however, many zoologists thought that insects could not receive sounds. Today it is generally admitted that sound production and sound reception occur widely in insects and that many important facets of their behavior are determined by sounds. The literature on these subjects has become quite large. In an admittedly incomplete bibliography, Frings (50) listed about 1200 references. There are at least twice this number, and almost one-fifth of these have appeared in the last ten years. For the Orthoptera alone, sufficient information was presented at a symposium on their acoustical behavior to result in a book-size publication [Busnel (22)]. With such a wealth of material available, it is obvious that this review can cover only a selected part of the recent literature.

Sound Production by Insects

Strangely enough, sound production by insects has not been adequately reviewed since the publications of Prochnow (103, 104), in 1907 and 1912. There have been short reviews such as those of Pringle (101, 102) or sections in textbooks, but these were not intended to be thorough. All insects produce sounds that are incidental to ordinary movements, such as flight tones and chewing sounds. In addition to these, the following specialized methods of sound production by insects are known: (*a*) tapping the substrate; (*b*) explosive expulsion of material through a small orifice; (*c*) snapping of a prosternal spine from a cavity in the mesosternum; (*d*) buzzing, whining or piping produced when the body is vibrated without flight; (*e*) rhythmic snapping of tymbals or tymbal-like organs; (*f*) stridulation; (*g*) expulsion of air over a specialized vibrating membrane. Of these, (*c*) is characteristic of Elateridae, and (*g*) is found only in a few Sphingidae, notably *Acherontia atropos* (Linnaeus). The other methods are more widely distributed.

Morphology of sound producing organs.—The morphology of most of the ordinary sound producing organs has been known for some time. Recent work has therefore been done mostly to aid in interpreting physiological studies. Such are the studies of Jacobs (72), Loher (83), and Pierce (95) for

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some Orthoptera, Ossiannilsson (91) and Pringle (99) for some Homoptera, and Schaller (119) for Corixidae.

Orthoptera ordinarily stridulate either by rubbing together specialized surfaces of the elytra (Tettigoniidae and Gryllidae) or by stroking the elytra with the hind femora (Acrididae). Kevan (77), however, has recently pointed out that Orthoptera use many other methods besides these to produce sounds. Some of these are: explosive expulsion of fluid; friction of the elytra against the abdomen or pronotum; snapping of the wings in flight; friction of the mid-legs against the elytra, and of the tibiae or femora of the hind legs against the abdomen. Kevan believes that the types he describes may be only a small fraction of the many that will be found in this order alone. This is supported by the discovery by Dansan (33), in the male of a wingless tettigoniid, *Eugaster spinulosus* (Johanssen), of an unusual, shelf-like mesothoracic stridulatory organ beneath a posteriorly projecting prothoracic shield.

Stridulatory organs are widespread among insects. For example, Eastop (37) has found a stridulatory surface on the abdomen of certain aphids that earlier field observers had reported as making sounds. Leston (79, 81) has devised a stethoscopic cage enabling him to study stridulation in various Pentatomidae. In this family alone at least six different types of stridulatory apparatus are now known. Hinton (63, 64) has described the means by which almost 100 species of lepidopterous pupae made sounds in the cocoon, mostly by rubbing together abdominal segments, hammering against the cocoon or substrate, or rubbing ridges or tubercles against the cocoon which may also be ridged. Thrips (Thysanoptera) might seem unlikely as sound-producers, yet Hood (66) has described a femoro-coxal rasp and file on the fore-legs of males of 14 species from three genera of thrips, and he suggests that these are true stridulatory organs. There are thus few orders of insects which do not have members known to produce special sounds.

Physiology of sound production.—With such diversity in structure, it is obvious that the sounds produced by insects are diverse. Sounds can be described physically by four parameters: frequency, intensity, wave form, and phase. For the sounds of insects, a fifth factor is also important—the temporal distribution of sound units. Most insect songs are complex, consisting of successive units joined to form larger units which may be still further combined, and so on. Unfortunately, the nomenclature for these units is still far from settled. A large number of terms is being used, viz., pulse, syllable, chirp, phonatome, stridulation, sequence, etc., and their foreign equivalents, but by no means for the same thing by different authors. An attempt has been made to standardize the terminology for describing insect sounds, at least those of Orthoptera, by Chavasse *et al.* (30), but it remains to be seen how widely this will be accepted.

The acoustical analysis of insect sounds ordinarily requires special apparatus. Sotavalta (123), however, determined the frequencies of flight tones

of insects through the use of his special gift of absolute pitch, but these tones are more or less simple. Since very few people have this gift, the method has little general utility. Hansson (56), Leston (81), and Ossiannilsson (91) have also used aural methods of analysis, but for limited objectives, and Hansson and Ossiannilsson checked with equipment. Busnel & Chavasse (19), Pierce (95), Pielemeier (93, 94), and others have shown that insects produce ultrasonic sounds or sound pulses at too rapid a rate for analysis by the human ear. Organoleptic analysis is thus risky and restricted in utility.

Electronic equipment is now usual for the analysis of insect sounds. A number of types of equipment have been used: oscillograph, which allows complete analysis [Hagiwara (54); Haskell (57, 60, 61); Lottermoser (84); Pringle (97, 99, 100); Sotavalta (123)]; tuned amplifier, which is useful for study of frequencies and rhythms [Pierce (95)]; modified oscillograph equipped with filters to analyze sounds in frequency bands [Busnel *et al.* 14, 19; Loher & Broughton (82)]; and sound-spectrograph, which produces a record of frequencies, intensities and temporal parameters simultaneously [Alexander (3); Borror (8)].

Some workers analyze the sounds as they are produced. It is far more convenient, however, to record the sounds for later analysis. Broughton (9, 10, 11) has used the disc recorder for this purpose. The tape recorder, however, with its wide frequency range, ease of operation, and low cost, is more convenient. The particular value of the tape recorder lies in the fact that continuous loops of recorded sounds can be prepared for repetitive display and analysis [Busnel (14); Busnel & Chavasse (19); Loher (83)]. Tape recordings can even be used directly to prepare visible patterns of recorded sounds by the use of special iron powder [Frings & Frings (46)].

Tape recording is easy in theory, but, if the recordings are to be used for careful physical analyses, the response curves of the microphones and the recording characteristics of the tape recorders must be known. Most commercial equipment is designed for use with voice or music, and the biologist thus should either be able to check his own equipment or have expert collaboration.

The tape recorder is also a valuable tool for playing back sounds, as acoustic dummies, to insects to study their reactions. When this is done, further problems may be encountered. Amplifiers and loud speakers used to project the sounds must be equivalent in fidelity to the recording equipment and equal to the task of projecting sounds with the essential acoustic elements. Thus, Busnel & Busnel (17) found that ordinary loud speakers failed to react rapidly enough to pulses of sound to afford adequate fidelity for female *Oecanthus pellucens* Scopoli, and they used a special corona-type transducer. Tischner & Schief (126) likewise found that the projection pattern of sound from a loud speaker is significant in studies with mosquitoes. On the other hand, sounds which to the human ear are quite poorly reproduced may induce reactions in insects [Haskell (57)]. High fidelity for man may not be high fidelity for insects, just as ultrasonic for man may not be

ultrasonic for insects [Autrum (6); Benedetti (7); Schaller & Timm (118); Treat & Roeder (128)].

Extensive studies on the stridulatory sounds of European Orthoptera have been made by Broughton (9, 11), Busnel (14), Busnel & Chavasse (19), Evans (40), Haskell (58, 60), Loher (83), Loher & Broughton (82), Lottermoser (84), and Pasquinelly & Busnel (92). A number of American species have been studied by Pierce (95). His method, however, allows accurate determination of temporal elements only. Frequency medians, as Pierce determined them, for broad band noises like those produced by most Orthoptera, are of little value. Busnel (14) and Loher (83) have noted that the idea of a median frequency is illusory, with variations depending even upon the leg used for stridulation [Busnel *et al.* (15)]. Loher (83) has shown that removal of teeth from the femoral comb in Acrididae or destruction of large portions of the elytra cause only a decrease in intensity of the sounds produced. Pierce's computations of the number of teeth struck and other characteristics from his records are, therefore, of questionable validity. Borror's (8) analysis of the song of *Neoconocephalus ensiger* (Harris) (Tettigoniidae) is accurate, but based on a limited sample. Frings & Frings (49) found clear-cut differences in the songs of different individuals in this species, confirming Loher's (83) report of individual variations in songs of Orthoptera.

Songs of Acrididae are generally broad band noises at 2 to 12,000 c.p.s. with maxima at 4000 to 8000 c.p.s. and intensities of 30 to 40 db, *re* 0.0002 dynes/cm^2., at 10 to 30 cm. [Busnel (14); Haskell (58); Loher (83); Loher & Broughton (82)]. Songs of Tettigoniidae are also wide band noises, but at higher frequencies, up to 100,000 c.p.s., with maxima at 8000 to 15,000 c.p.s. and intensities of 45 to 70 db [Borror (8); Busnel (14); Busnel & Chavasse (19); Pasquinelly & Busnel (92); Pielemeire (93, 94); Pierce (95)]. Songs of Gryllidae, including *Oecanthus*, are relatively pure tones at 2000 to 6000 c.p.s. and intensities of 40 to 60 db [Alexander (3); Busnel (16); Haskell (57); Pasquinelly & Busnel (92)].

Busnel (23) believes that, in Acrididae, the lower frequencies and intensities and the variety of forms which the songs take [Faber (42)] are related to the problems of communication in environments with high population densities and many acoustic obstacles. Conversely, in Tettigoniidae and Gryllidae, the higher intensities and frequencies and the relative simplicity of the calls are related to the fact that population densities are low and many of these insects mount higher objects for singing. This interpretation of the facts, however, does not apply for the Acrididae tested by Haskell (58), if the sensitivity of the tympanal apparatus is considered in computing the acoustic field for each species.

As illustrations of the analysis of the songs of Orthoptera, we have selected two studies: Busnel (16) on *Oecanthus pellucens* and Pasquinelly & Busnel (92) on *Ephippiger bitterensis* Finot (Tettigoniidae). The song of *O. pellucens* can be analyzed temporally into successive stridulations, consist-

ing of trills, which vary in number depending upon the type of song. Each trill is produced by 6 to 20 oscillations of the elytra. The frequency is 2000 to 3000 c.p.s. and relatively pure. The tooth impact frequency is synchronized with the resonant frequency of the elytra, thus producing one sound wave per tooth impact. The intensity at 10 cm. is quite variable (42 to 66 db) and not clearly related to the type of song or physiological state. The song of *E. bitterensis*, on the other hand, consists of pulses of broad band, high frequency noise, with each tooth impact producing one chain of complex waves which decays exponentially before the next chain starts.

In cicadas, sounds are produced by a pair of tymbals at the base of the abdomen of the male. Ossiannilsson (91) has reported a comparable situation for leafhoppers. Pringle (97, 98, 99) and Hagiwara (54) have made detailed studies on sound production in cicadas. Each tymbal has an attached muscle which snaps the tymbal in. The snapping in of the tymbal when the tension reaches a critical value produces a click, and the snapping out as the muscle relaxes, apparently because of the sudden release of tension, also produces a click.

Pringle (97, 98, 99) studied the Ceylonese species, *Platypleura capitata* (Olivier) and *Platypleura octoguttata* (Fabricius). By placing electrodes on the tymbal muscles, he was able to stimulate them with pulsed shocks at various rates. He found that these muscles, like the flight muscles, have a myogenic rhythm: continuous activity is maintained by nerve impulses which are not synchronized with the contractions of the muscles. The song thus produced is a series of damped oscillations. For *P. capitata* the fundamental sound frequency is about 4500 c.p.s., and the pulse repetition rate 390/sec. For cicadas in general, if the damping is rapid, man hears the pulse rate (120 to 600 c.p.s.); if the damping is slow, man hears the fundamental frequency of the tymbal vibration, with the pulses modulated on it. If, in the latter case, the pulses are coherent in phase, man detects a harmonic chord; if the pulses are not coherent, one hears a noise, like a hiss. A tensor muscle attached to the tymbal maintains the elasticity and by differential tension, alters the mechanical properties of the tymbal. Abdominal air sacs, which are tracheal in nature, form a resonant cavity the acoustic properties of which can be changed by changing the size.

Using this knowledge, Pringle (99, 100) interpreted tape recorded and oscillographically analyzed songs of a number of cicadas in terms of variations in rhythm of the tymbal muscles, tension of the tensor muscles, and size of the air sacs. Two species in the genus, *Terpnosia*, are almost indistinguishable morphologically, but their songs allow them to be easily separated.

Hagiwara's (54) studies on nerve and muscle potentials during shrilling in cicadas check Pringle's reports quite well. He reported, for *Platypleura kaempferi* (Fabricius), that the tymbal muscles behave like flight muscles. For *Graptopsaltria nigrofuscata* Motschulsky, *Oncotympana maculaticollis* Motschulsky, and *Tanna japonensis* Distant, however, he found a one to one

relationship between nerve impulses and clicks of the tymbal, and for *Meimuna opalifera* Walker, an intermediate condition. In *G. nigrofuscata*, damped oscillations are produced by a single tymbal at a rate of about 100/sec. The tympana on the two sides of the body alternate with each other, however, to produce sound pulses at about 200/sec. As Pringle (99) notes, it is remarkable that such a diversity of patterns of coordination should have evolved in this family with so little modification of the basic anatomical plan.

Flight tones of insects have received attention, but mostly because of interest in flight itself [Sotavalta (123)]. These have a fundamental frequency which is the same as the wing-beat frequency, with modulated secondary frequencies depending upon other factors. The frequencies for different insects range from 5 to 1046 c.p.s., and intensities are likewise variable. In many insects, flight tones are merely incidental sounds, but in some, such as mosquitoes [Roth (116); Tischner (125)], they have biological uses.

Much discussion has centered about sounds produced by many insects when not in flight which sound like flight tones but are about one octave higher. Sotavalta (123) calls these "whining" tones; others have used other terms. In the honey bee, queens and occasionally workers produce these sounds, called piping and qualking sounds. Sotavalta, with Prochnow (104) and others, believes that these result from vibrations of the thorax by the flight muscles. Woods (136), however, believes that they are produced by movement of air through the spiracles, presumably driven by the activity of the flight muscles.

Effects of the environment on sound production.—Insects which stridulate usually do so at certain times of the day. At present, there is no unequivocal demonstration that light per se is the most important factor, although this seems likely. However, concomitant changes in relative humidity and temperature may be important. The microclimates of singing insects deserve much more careful study than they have received, for they not only have direct effects on behavior, but also may determine the effective communication distances of the songs [Busnel (23); Haskell (58)].

The effects of temperature on the songs of gryllids, tettigoniids, and leafhoppers have recently been studied. Jacobs (73) indicated, in a preliminary report on *Gryllus campestris* (Linnaeus), that the number of pulses in 10 sec. is a direct function of temperature, as in *Oecanthus niveus* De Geer, sometimes called the temperature cricket [Hallenbeck (55)]. On the other hand, Ossiannilsson (91) found thermal optima for call rates in three species of leafhoppers; the sound frequency increased with rising temperature. Frings & Frings (49) studied the chirp rate of the tettigoniid, *Neoconocephalus ensiger*, by recording at different temperatures and playing the tape recordings at reduced speeds. The relationship between chirp rate and temperature is exponential in this case. They suggest that this may be the situation for other species if studies are made with controlled temperature changes, instead of under field conditions. The gradual changes in the field

might allow the insects to adapt to different base rates, as Bullock (13) has noted in many invertebrates. Certainly much work remains to be done on the effects of environmental factors on sound production in insects, particularly statistical studies to determine variability, before broad generalizations will be possible.

Sound Reception in Insects

Reviews on this subject have been published in recent years by Autrum (6), von Buddenbrock (12), Dethier (35), Pumphrey (105, 106), Rau (110), and Wigglesworth (135).

There has been much debate about "hearing" in insects, most of it about the definition of hearing. The matter is discussed by Rau, Pumphrey, von Buddenbrock, and Chrysanthus (32). While it is admitted that many insects respond to sounds, there is disagreement on whether this is actually "hearing" or tactile reception. Von Buddenbrock takes the view that hearing means reception of air-borne sounds through specialized receptors only; other reception of sound involves a vibration-sense (Erschütterungssinn). Pumphrey, on the other hand, includes under "hearing" oriented reactions to sound in any medium whether mediated by specialized receptors or more generalized mechanoreceptors. We adopt Pumphrey's ideas, believing that reception of periodic compressional waves in gases, liquids and solids may occur through a number of different organs on the insect body.

In recent years, evidence for sound reception by a wide variety of receptors other than recognized tympanal organs has accumulated: scolopidial organs in the legs of many insects [Autrum & Schneider (5)]; proprioceptors, probably scolopidia, in body-wall of *Dytiscus* and *Locusta* [Hughes (70)]; Johnston's Organs in the antennae of mosquitoes [Roth (116); Tischner (125)]; tactile hairs on the cerci and abdominal sclerites of locusts [Haskell (60)]; aristae of the antennae of muscoid flies [Wellington (134)]; and trichobothria of spiders [Chrysanthus (32)]. Thus, unless one makes arbitrary distinctions between reception of sound and reception of other periodic deformations, it seems necessary to regard all mechanoreceptors as potential sound receptors. Only when information is gathered on the ability of insects to use these for analysis and localization of sounds will it be possible to distinguish between "hearing" and other sensory modalities, if, by then, such a distinction will even seem necessary.

The tympana and auditory hairs of insects are displacement receptors, not pressure receptors as are the ears of vertebrates [Pumphrey (105); Autrum (6)]. A characteristic of sound receptors of this type is individual directional sensitivity, because displacement is a vector quantity. Thus an insect can, with one tympanum, localize sounds. These receptors apparently lack means for frequency analysis and act chiefly as rectifiers for the pulsed sounds which insects characteristically produce.

Scolopidial (chordotonal) organs.—In the Orthoptera, these are found in

the specialized tympana. Haskell (60, 61) has recently made a critical electrophysiological study of sound reception in four species of Acrididae. The nerve impulses produced by stimulation with pure tones are asynchronous with the sound frequencies. The tympanal organs respond to pulsed sounds with synchronous volleys of spikes up to 90 to 100 pulses/sec.; above that synchronization ceases. Using stridulatory and imitation stridulatory sounds, Haskell found that volleys of spikes in the nerves follow the pulse frequency of the incoming signals. The critical parameter for these organs would seem to be, as Pumphrey had earlier reported, the modulated pulse frequency.

Pringle (97, 99) has made a similar study on the tympanal organs of male and female cicadas in conjunction with his studies on sound production. When a tympanum is stimulated with the recorded sound of other cicadas, the scolopidial elements produce volleys of nerve impulses that are synchronous with the pulses of sound in the signal. Thus this organ also is sensitive to pulse modulation and is similar in physiology to that of the Orthoptera. During singing, the tympanum is creased by a tensor muscle which protects it against the high intensity sound nearby.

Schaller & Timm (118) first demonstrated unequivocally that the tympanal organs of moths receive sounds which are ultrasonic for man. They studied 38 species from the families, Phalaenidae, Geometridae, Notodontidae, and Arctiidae. When stimulated with the sounds, resting moths sprang into flight and flying moths stopped flying. Maximal responses were obtained at 40,000 to 80,000 c.p.s. They believe that these reactions enable the moths to escape capture by bats, an idea previously suggested, but without proof of reception of bat sounds by moths. Treat (127) later studied reactions of a number of species of moths which were tethered so that their reactions could be followed kymographically. He used a Galton whistle with maximum output about 24,000 c.p.s. for stimulation. Reactions like those obtained by Schaller & Timm were observed and studied.

Haskell & Belton (62), using electrophysiological means, found responses to high frequency but not ultrasonic (3000 to 20,000 c.p.s.) tones in the tympanal nerves of notodontid and arctiid moths. Treat & Roeder (128) have similarly found responses in the tympanal nerves of some phalaenid moths, chiefly *Prodenia eridania* (Cramer), at frequencies of 3000 to 240,000 c.p.s. The maximum sensitivity is at 15,000 to 60,000 c.p.s., with no evidence of frequency discrimination. There is an afterdischarge following sound pulses, and adaptation is rapid. The tympanum, therefore, seems to be an effective pulse receptor. It is sensitive to the cries of bats, sonic or ultrasonic, and is thus probably used by moths as a detector of bats.

In *Corixa striata* Linnaeus, a specialized tympanum is found on the mesothorax in an air-filled space beneath the wings. Schaller (119) has studied its sensitivity by behavioral means. Males and females respond to sounds from 2000 to 40,000 c.p.s.; the tympanum is necessary for responses. This tym-

panum possesses an externally projecting club, somewhat like a halter. Removal of this structure does not destroy the power to receive sounds, and Schaller believes that the club acts as an amplifier for vibrations of the tympanum.

Among other specialized forms of scolopidia, the greatest amount of work has been done on the Johnston's Organs of the antennae of Culicidae. Roth (116) has shown, through behavioral experiments, that the Johnston's Organs of the antennae of male *Aedes aegypti* (Linnaeus) are receptors for vibrations of the antennae produced by sounds. The males respond maximally at the fundamental wing-beat frequencies of the females. That a similar situation may exist in Ceratopogonidae has been suggested by Downes (36), who found that the males in mating swarms erected the hairs on the antennal flagellum, as Roth had observed for *Aedes*. Tischner (125), and Tischner & Schief (126), using electrical impulses from the Johnston's Organs of male *Anopheles subpictus* Grassi, found that the audiogram thus determined peaks at the wing-beat frequency of the female. Furthermore, sounds directed parallel with the flagellum of the antenna produce maximal nerve potentials, while sounds directed perpendicular to the flagellum produce similar potentials at a much reduced intensity. Thus, they believe, even a single antenna allows localization, as with other displacement receptors. Risler (115) has studied the morphology of the Johnston's Organs in *Anopheles stephensi* Liston, and he and Tischner have related the findings to the electrophysiological results. The electrophysiological studies of Uchiyama & Katsuki (129) and Schneider (120) indicate that the Johnston's Organs in *Locusta migratoria* Linnaeus and *Bombyx mori* (Linnaeus) repectively may also be capable of sound reception.

Generalized scolopidia without tympana are able to receive sounds carried through the substrate, or through air [Debaisieux (34)]. There are a number of studies on the structure and distribution of these, such as Richard's (111, 112, 113) on termites and McFarlane's (85) on *Melanoplus*. Autrum & Schneider (5), and Schneider (121) have used electrophysiological methods to study these organs in the appendages of a number of species of Orthoptera, Hemiptera, Coleoptera, Diptera, Lepidoptera, and Hymenoptera. Insects with subgenual organs (Orthoptera, Lepidoptera, Hymenoptera) are exceedingly sensitive to "vibrations"; those without subgenual organs (other orders tested) are far less sensitive. The subgenual organ seems to be a specialized receptor which transforms signals above 400 c.p.s. into asynchronous nerve discharges. In honey bees, Hansson (56), using conditioning methods, got only slight evidence of training with sounds, and for that it was necessary to have the bees walk over a vibrating platform. He also showed that high intensity sounds directed at the hives of bees could cause decreased activity. Frings & Little (48) confirmed the latter observation and believe, as does Hansson, that reception is through the legs, probably mediated through scolopidial elements.

Scolopidia in the body-wall of *Dytiscus* and *Locusta* also respond to air-borne sounds, or at least to vibrations of the body produced by the sounds [Hughes (70)]. Similar organs are probably involved in responses of the butterfly, *Cercyonis pegala* Fabricius (Nymphalidae), to air-borne sounds at high intensities, although tactile hairs or muscle proprioceptors may also be active [Frings & Frings (47)]. This observation may explain the residual reactions found by Treat (127) and others in moths with the tympana destroyed, and it shows the importance of knowledge of intensity of sounds in studies on phonoreception.

Tactile hairs.—Haskell (60) has studied responses in the nerves of four species of Acrididae to stimulation of hair sensilla by sounds either through the air or the substrate. The long hair sensilla on the cerci respond to gross air movements with bursts of spikes and to pure tones up to 300 c.p.s. with synchronous discharges. Their small frequency range and limited numbers make them probably of little use to the locust in reception of natural sounds. Responses in the segmental nerves of the third thoracic ganglion when the animals are stimulated by vibration of the substrate or air-borne sounds are probably produced by hair sensilla on the abdominal sternites or pleura. These would seem to be of considerable importance in reception of vibrations in the substrate [Ellis (39); Haskell (59)].

The possible sound receptors of locusts thus include, besides the tympanal organs: hair sensilla on the sternites and pleura, cercal hair sensilla, scolopidia in appendages [Autrum & Schneider (5); McFarlane (85)]; scolopidia in the body wall [Hughes (70)]; the Johnston's Organs of the antennae [Uchiyama & Katsuki (129)]; and specialized hair sensilla in patches on the face which are sensitive to vibration of moving air and mediate responses in flight [Weis-Fogh (132, 133)]. With such an array of receptors, it is no wonder that even fragments of locusts respond to air-borne sounds of relatively high intensity by startle reactions [Busnel & Busnel (18)]. The similarity between the aerodynamic organs of locusts, as described by Weis-Fogh (133) and the Eltringham's Organ of Lepidoptera and Trichoptera studied morphologically by Ehnbom (38) leads one to the suspicion that the latter may act as a sound receptor, but the matter has not been tested.

Other receptors.—That muscle proprioceptors described in lepidopterous larvae by Finlayson & Lowenstein (43) and Acrididae by Slifer & Finlayson (122), and the campaniform sensilla, studied so admirably as proprioceptors by Pringle (96), could respond to sound waves which vibrate parts of the body is almost certain, but so far there has been no demonstration of this.

Acoustical Behavior of Insects

Terminology.—Faber (42) has recently extended his earlier scheme for classifying the communication signals ("language") of Orthoptera. This scheme has been widely used. Faber's guiding principles are well presented

in a paper in 1952 (41). Briefly, he proposes to study behavior patterns, particularly those related to sound, as earlier morphologists studied structures. They studied forms in space; he proposes to study forms in time (*Zeitgestalten*). These, he believes, can be treated just like the space forms—homologies and analogies found, fundamental forms and their modifications described, and the whole systematized and related to the physiology and phylogeny of the animals.

Faber's earlier classification of the communicative means of Orthoptera was relatively simple. He recognized the following sounds (English equivalents used by different authors in parentheses): (*a*) *Gewöhnliches Gesang* (Ordinary, Usual, Wonted, Calling, Spontaneous, Indifferent, Solitary, Common Song); (*b*) *Rivalengesang* (Rivals' Song, Rivals' Duet); (*c*) *Werbegesang* (Courtship Song, Serenade); (*d*) *Anspringlaut* (Nuptial Song, Shout of Triumph); (*e*) *Paarungslaut* (Sounds during Mating); (*f*) *Störungslaut* (Alarm Cry); (*g*) other sounds associated with special activities and derived mostly from those already listed. A special type of Ordinary Song, in which individuals alternated or sang together (*Anaphonie* or *Allelophonie*), was called *Wechselgesang*.

In 1934, for 65 species of Orthoptera, Faber found over 300 individual communicative sounds, as well as many postural communicative signals. In 1953, he has 28 fundamental types (*Grundtypen*) of sound signals, many of these subdivided, so that the system is quite complex. At the same time, the rigid categorization does not take into account the existence of manifold variations and intergrades in communicative sounds [Jacobs (73); Loher (83)]. Many workers still use some modification of Faber's scheme, but it seems unlikely that this recent elaboration will gain wide acceptance.

Jacobs (71, 72), in his reports on European Acrididae, uses a modified form of Faber's nomenclature for their sounds, and terminology like that of Lorenz and Tinbergen (124) for description of their behavior. The problems involved in using this terminology for studies of Orthoptera are discussed by Pumphrey (107).

Busnel (24) and his co-workers utilize nomenclature for reactions to sounds derived from the earlier students of orientation of animals [Fraenkel & Gunn (44)]: phonokinesis, phonotaxis, phonotropism, etc. For the songs, they generally employ a modified form of Faber's nomenclature.

Sounds of uncertain function.—Some earlier workers on insect sounds regarded them as merely accidental by-products of other activities. Although there are sounds produced by insects which may have no special function, it seems unlikely that specialized sound producing organs would be evolved without some utility to the insect. Currently, therefore, intentional sounds of insects are assumed to have some function, although we may not know certainly what it is. The stridulation of lepidopterous pupae, for instance, seems most likely to be defensive in nature [Hinton (63, 64)], for no other purpose seems possible, and the pupae only stridulate when disturbed. An

acoustical defensive adaptation of another type was noted by Gaul (52) in the audio-mimicry shown by a syrphid fly which resembles a wasp. Analyses of the wing tones of the two species showed that these were almost exactly alike.

Responses of insects to sounds of other species.—Two common patterns occur: feeding responses and avoidance responses. As an example of the first, Richard (114) has found that ant lions (Myrmeleontidae) react to their prey by vibrations received through receptors on or in the first thoracic segments. As an example of the second, Schaller & Timm (118) and Treat & Roeder (128) have demonstrated responses to ultrasonic cries of bats in a number of species of moths with tympana.

Acoustical communication in insects.—A well-known phenomenon in the reactions of insects to light is the kinetic effect of the stimulus. A similar effect for sound has been suggested by Ellis (39) for marching grasshoppers, *Locusta migratoria*, by Haskell (57) for *Gryllulus domesticus* (Linnaeus), and by Rabe (108) for *Notonecta glauca* Linnaeus.

Communication for nonreproductive purposes has been studied in a few species. Haskell (61) made a combined laboratory and field study on the factors determining general swarm cohesion, return to a flying swarm (Edge Effect), and mass take-off in the desert locust, *Schistocerca gregaria* Forskål. The response of the tympanal organ to flight noises of other locusts was studied electrophysiologically and found to consist of bursts of nerve impulses at the frequency of the wing cycle. The sounds of flying individuals and swarms were recorded and analyzed. The general swarm noise is a random noise, but individuals produce pulses corresponding with the wing-beat. Playback of recorded wing-beat noise to settled swarms only rarely results in reactions. Deafened locusts can fly normally, but occasionally do not take off. In general, the wing-beat noise seems to be a stimulus, but other sensory input apparently is involved in swarm cohesion. Further study will be needed to clarify the situation.

The communicatory dances of honey bees are well known. It is also well known that bees produce a number of sounds, some of which are characteristic of certain activities. The piping and qualking of queens are particularly striking and, since the queens answer each other, would seem to be involved in communication [Allen (4); Woods (136)]. So far, however, the exact purpose of the auditory displays of queens has not been determined. Hansson (56) investigated the flight sounds of worker bees and found that, while certain sounds accompany certain activities, the frequencies are determined chiefly by the flight speed and loading of the bee. At any rate, flight tones under different conditions overlap so much in frequency that it seems unlikely that they could be used as signals. The fact that he could find no evidence of reception of sounds by the bees in flight further supports this idea. He did find that the bees could receive vibrations through solids, and

thus the piping of a queen apparently reaches other queens. Lecomte (78) found that aggregation in worker bees is brought about by low frequency vibrations through the substrate produced by other bees, as well as by odor and possibly other stimuli. A critical evaluation of the place of sounds in the life of bees, however, awaits further work.

The recent literature on sexual behavior of Orthoptera, in which sounds play a major role, is too vast for adequate review in a small space, and only selected examples can be cited. Detailed descriptions can be found in the large publications of Faber (42) and Jacobs (71, 72) on many European Acrididae and Tetrigidae, the papers of Weih (131) on *Chorthippus* spp. (Acrididae) and *Omocestus* spp. (Acrididae), and of Zippelius (137) on *Liogryllus campestris* (Linnaeus) (Gryllidae) and *Metrioptera* spp. (Tettigoniidae), and the articles of Busnel and co-workers (17, 20, 21, 29), and Loher (83) on *Ephippiger* spp. (Tettigoniidae), *Oecanthus pellucens* (Gryllidae) and *Chorthippus* spp.

One question of great interest is: what are the effective parts of the acoustic signals for Orthoptera? The point has been studied by Haskell (60), using electrophysiological methods; by Busnel (24, 26), Busnel & Loher (25, 28) and Loher (83), using reactions of males and females to artificial and and recorded natural sounds; and by Jacobs (72, 73) and Weih (131) through field observations. Modulated sounds or sounds with broken intensity patterns apparently carry maximum information for insects. Specific recognition in most cases depends upon the rhythm of response produced in the afferent nerves by the modulation envelopes or pulse frequencies. Busnel (24, 26) believes that the effective stimulating element in artificial sounds is the presence of sudden changes in intensity (transients), but the work of Haskell (60) indicates that these act merely, if correctly spaced, like modulated frequencies.

The importance of non-air-borne vibratory stimuli is becoming increasingly clear. Haskell (59) has shown that female *Chorthippus parallelus* (Zetterstedt) with tympana destroyed can detect stridulation nearby, probably by reception of vibrations in the soil. In some Acrididae, the sexes signal to each other by drumming with the feet [Faber (42); Jacobs (72)]. In *Ephippiger*, the males call the females by a song, and when a female reaches the plant on which a male stands the two conduct a "conversation" by trembling motions carried through the plant [Busnel *et al.* (29)].

It was once thought that most female Acrididae and Tettigoniidae are silent, but this may not be correct. Ragge (109) has discussed female stridulation and finds that it occurs only when the female is ready for copulation. Thus, in nature it occurs only for a short time and is easily missed. The stridulatory organ in sound producing females is poorly developed and the sound is lower in intensity than in males. The studies of Busnel (14), Faber (42), Jacobs (71, 72) and Loher (83) all give evidence of the importance of

stridulation of female Orthoptera in sexual communication. In some cases, the female is silent, but goes through the motions of sound production in answer to the male [Huber (69)].

The communication signals of Orthoptera usually bring about responses only intra-specifically. The receptors of similar Orthoptera, however, are similar in sensitivity, and signals from one species are probably received similarly by others. Differentiation between signals by the insects would thus seem to be made in the central nervous system [Haskell (60); Jacobs (72, 73); Loher (83)]. Some direct evidence is now available. Huber (67, 68) determined the effects of extirpation of parts of the nervous system on mating behavior in *Gryllus campestris* and *Gomphocerus rufus* (Linnaeus) and found that the "mushroom bodies" in the brain are essential for normal singing. Busnel & Loher (21) found, in male *Chorthippus biguttulus* (Linnaeus), evidence for directional memory. The male signals and, if the female answers, he starts toward her. Since he must traverse tangled grass, his path is tortuous, and within 3 to 5 sec. he signals again. If the female again answers, he keeps his bearing for 3 to 5 sec. more, and so on. On the other hand, the female *Ephippiger* seems to move reflexly, her speed of travel over clear ground toward the continuously singing male is determined by the intensity of the sound according to the Weber-Fechner Law [Busnel *et al.* (29)].

Sounds are also known to play a role in mating responses of certain Diptera. Kahn *et al.* (74, 75, 76, 90), Roth (116), Roth & Willis (117), and Tischner *et al.* (125, 126) have demonstrated that male mosquitoes respond to frequencies of sound like those of the female wing sounds or to recordings of these wing sounds. The receptors, as shown by the extirpation experiments of Roth, are the Johnston's Organs of the antennae. Muspratt (87) also found that male *Aedes aegypti* are attracted to buzzing females of *Megarhinus brevipalpus* (Theobald) in a cage, and Nielsen & Greve (89) attracted swarms of male mosquitoes by singing certain notes. The specific identifying factor in these signals is not obvious, for the range of wing-beat frequencies of female mosquitoes of different species is not great. Perhaps, as Nielsen & Greve (89) suggest, the females are attracted to the male swarms.

A similar situation seems to exist in Ceratopogonidae [Downes (36)] and Chironomidae [Gibson (53)]. Monro (86) and Myers (88) have reported that male fruit flies (Trypetidae), *Dacus tryoni* (Froggatt) and *Dacus cacuminatus* (Hering), produce a sound which attracts females for mating, and Vanderplank (130) found that interspecific mating in tse-tse flies, *Glossina* spp., is possible if frequencies of sound like those of the female's wings were used to induce mating responses in males. Intersexual signalling with wing sounds may therefore be common in Diptera.

In Hemiptera, Leston (80) and Schaller (119) have shown that the stridulation of male Corixidae attracts the females for mating. The sound is re-

ceived through the tympanal organs. Like the Orthoptera, the males answer artificial sounds or the calls of other males. In Homoptera, Ossiannilsson (91) reported that male leafhoppers produce a Common Song to attract the females, a Courtship Song, and Calls of Rivalry. Females produce a Call of Invitation and both sexes produce Calls of Distress. Other calls he was unable to classify. The males answer each other, but Ossiannilsson could find no specialized sound receptors. Alexander (3) and Pringle (99) believe that the singing of cicadas is in the nature of an Ordinary or Congregational Song and serves to assemble local populations into small groups for mating.

Evolutionary significance of acoustical communication.—Insect songs are widely various, although, within each group, are often variants of basic acoustic patterns [Faber (42); Pringle (99)]. Since these bring the sexes together for mating in many species of Orthoptera, some Diptera, and some Homoptera, interest attaches to the means by which each species distinguishes its own song.

Busnel *et al.* (27) have found that different species of *Ephippiger* react to each other's signals and imply that discrimination may be very poor. They admit, however, that the species which cross-mated in their tests are separated geographically in nature. Loher (83) has found that the ability to discriminate varies among species of *Chorthippus*, and Haskell (60) believes that this is related to the complexity of song in the various species. Further work is needed to determine the true limits of discrimination in many species.

In insects which use acoustic communication signals, behavioral isolation may be an important factor in evolution [Alexander (3)]. If behavior patterns which effectively prevent cross-mating arise, it would be merely a matter of time until genes with structural effects would accumulate within the separate strains. Studies of hybridization, such as the preliminary investigations of Fulton (51) and von Hörmann (65) on some Gryllidae, would be valuable for interpreting the possible evolutionary significance of insect songs. At present, we have too few data to warrant generalizations.

The differences in acoustical behavior between different species of insects are as specific as the more usual morphological features. Thus, Jacobs (72), on the basis of such differences in certain Acrididae, decided that three of the species he studied should be transferred from the Acridinae to the Oedipodinae, and Chopard (31) has suggested that songs may be essential for separating species or races of Gryllidae. Certainly, with improved facilities for recording and storing samples of insect songs, fruitful studies on these lines will be possible.

Possible practical utility of sound in insect control.—So far, there has been little to encourage even the most enthusiastic. Adams *et al.* (1, 2) have used sounds produced by feeding granary weevil larvae to find infestations. Frings *et al.* (45) have killed insects with very high intensity sounds, but the cost of this is prohibitive. Kahn & Offenhauser (75, 76) reported success in attracting male mosquitoes to a charged grid and thus to death, but their

tests were pilot studies and, after ten years, no large scale practical tests have been made. With the reproductive potential of female mosquitoes what it is, and the fact that the sound must compete with the natural attractant under adverse conditions, for it cannot be too loud, the method seems to hold little promise.

If sonic repellents could be found—and particularly if the frequencies were ultrasonic for man—they might have great value. So far, in spite of anecdotal reports that circulate in the press, there has been no demonstration of a practical sonic insect repellent.

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DYNAMICS OF INSECT POPULATIONS[1]

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Probably the most contentious question concerning animal ecology at the present time is whether animal populations are self-regulating or not. Thompson (23) and Solomon (20) have already discussed this question in this *Review*, from very different standpoints, and they have reached almost diametrically opposite conclusions. Although I agree in general with Solomon's views, I do not hesitate to raise this question again. It is important that every effort should be made to resolve it unequivocally, for confused ideas upon this subject have bedevilled ecological theory for many years.

There is a prevalent idea that the differences between the two schools of thought are mainly verbal. True, there is much in common, but there is also a very real difference. One school holds that density-governing reaction is an essential mechanism for the control of populations, whereas the other considers that it is not essential, and that it seldom, if ever, controls populations. Here there is no possibility of finding common ground. I propose, therefore, to present a brief summary of the evidence for the existence and universal operation of density-governing reaction in population control, then to examine the criticisms which have been levelled against this, and later to discuss the alternative mechanisms of control which have been suggested.

The Self-Regulation of Populations

Howard & Fisk (10) are considered to be the first entomologists to recognize clearly that, of the numerous factors which influence the mortality and natality of insects, only those which act with increasing severity as populations become larger are capable of adjusting populations to their environments. Many other biologists have since expressed and elaborated the same idea. For many years it has been usual to speak of those factors which operate with increasing intensity as a population grows as "density-dependent factors," and to those which do not do so as "density-independent factors." As has already been shown [Nicholson (15, p. 16)], these terms are somewhat misleading, and their misuse has led to confusion at times: I shall use them in this article only wherever change in terminology might confuse discussion of the views and explanations of other biologists.

The distinction drawn by these two terms is one of function, not of importance, as seems often to be thought, for factors of both kinds may play important parts in the regulation of populations. There is a strange and prevalent idea that those biologists who insist that "density-dependent factors" uniquely have the function of governing the size of populations be-

[1] The survey of the literature pertaining to this review was completed in May, 1957.

little the part played by "density-independent factors," particularly climate, by so doing: yet, when an engineer stresses the importance of the pendulum in governing the speed at which a clock's mechanism operates, no one thinks he denies the importance of the main spring, or of the gears.

To assist later discussion I shall briefly outline the mechanism of self-regulation in populations. Each species of animal is necessarily limited to those regions in which everything it requires is supplied in a quantity, and of a quality, not less than the minimum necessary for continued existence and for reproduction at the replacement rate. Outside such regions the inherent resistance of the environment prevents the continued existence of the species. Inside these regions the animals tend to increase progressively, but this increase automatically induces additional resistance to multiplication. This induced resistance is commonly the depletion of one or more requisites; but it may take other forms. It may be an induced increase in the number of natural enemies, in which case the prey animals are the governing requisite of their natural enemies, or, instead of depleting requisites, the animals may cause a qualitative deterioration in these—for example, by the accumulation of harmful metabolites. In addition, crowding may directly increase mortality or decrease fertility, even though all requisites remain adequate.

It is this interplay between the multiplication of animals when conditions are favourable and the consequent induction of resistance, which enables populations to adjust themselves automatically at, or about, densities related to their own properties and to those of their environments. Such automatic counterbalancing of the tendency to increase progressively enables populations to persist in a stable state in widely different, and even violently fluctuating, environments [see Nicholson (15) for fuller description of this mechanism].

Note that such adjustment is not necessarily operative at all times. For example, if a population is reduced to a very low level, due to some adverse factor (which in temperate regions may be no more than a change of seasons) the population must be expected to multiply without check for some time after favourable conditions return; opposition to population growth only begins when the population becomes sufficiently high to cause significant depletion, or some other density-governing reaction.

When there is a gradient from inherently favourable to unfavourable conditions, the mechanism described permits a species to persist indefinitely in all favourable places; and it causes the intensity of induced resistance to fall towards zero as the limits of favourability are approached. Consequently, near the fringes of distribution, density-governing reaction must be slight and inconspicuous.

Individuals of most populations tend to diffuse out of favourable places into the surrounding country and many species can maintain themselves permanently in fringing zones where favourability is below the threshold level—the inability of the resident animals to replace themselves by reproduction being offset by the continual immigration from neighbouring favourable places. Note that, although density-governing reaction may not occur

in these fringing zones, it is ultimately responsible for the limitation of density there. This is because the number of immigrants is a function of the size of the population in the favourable place from which these emigrated, which itself is adjusted by density-governing reaction.

Field evidence for self-regulation.—Because of shortage of space I shall limit attention to a few examples of field studies of which I have some personal experience. A spectacular example of how animals may limit their own numbers by the density-governed ajustment of their main requisites to the threshold level (which approximates to the minimum necessary for their continued existence) was provided by the introduction of *Cactoblastis cactorum* (Berg) into Australia for the control of "prickly pear" (*Opuntia inermis* and *O. stricta*) [Dodd (6)]. Before the introduction of *C. cactorum* prickly pear occupied millions of acres in Queensland, often in almost pure and impenetrable stands. After its release *C. cactorum* multiplied with extreme rapidity, soon reaching such densities locally that the whole of the prickly pear above ground was destroyed, and millions of partly fed larvae were seen to wander around and die of starvation. During the next two or three years there was some regrowth of prickly pear, for *C. cactorum* had almost ceased to exist; but this insect very quickly multiplied from its small residual numbers and destroyed the regrowth. This sequence of events continued over the whole infested area in Queensland. In a recent discussion, Mr. Dodd informed me that the position for many years had been that, throughout the originally heavily infested areas, very small groups of prickly pear are seen only occasionally, and these are inevitably found before long by *C. cactorum* and destroyed, so exemplifying the type of "spotty distribution" which has been shown [Nicholson (13)] to be a probable end result of the interaction between an effective specific parasite and a specific host. Occasionally, in areas which are far from any resident *C. cactorum*, patches of this weed may develop and infest several acres in the course of a few years. Sooner or later however, these patches are inevitably found by *C. cactorum* and destroyed completely.

An essentially similar course of events has been observed in each instance where biological control has proved effective, whether against weeds or insect pests [see Sweetman (21); Imms (11)]. Each natural enemy reduced its prey or food plant to such scarcity that difficulty was experienced in finding enough to permit the production of offspring at the replacement rate. On the other hand, the food plant, or prey, while still at a low level, limited its own density by maintaining a sufficient density of enemies to destroy the surplus of offspring it produced.

Many other kinds of density-induced governing reactions have been observed. For example, field studies have shown that blowflies, although often heavily attacked by predators and parasites in their earlier stages, are found to limit their populations by intense competition amongst the larvae for food [Fuller (9), Salt (18), and Ullyett (24)]. The effect of such intense competition is to reduce the number of adult flies emerging from a carcass far below that which the same amount of food could maintain were

there no competition. Fuller (9, p. 31) showed that sheep carcasses buried two days after death gave rise to far more blowflies than unburied carcasses, evidently because of the smaller numbers of eggs laid upon them and the consequently lessened intensity of larval competition.

Similarly Carne (2) has shown recently that strife between the crowded larvae of *Aphodius howitti* Hope reduces the number of survivors in a unit of area to approximately the same figure irrespective of the degree of crowding. Such density-induced mortality accounts for the destruction of almost the whole of the surplus offspring produced by *A. howitti*, and clearly regulates its abundance. In this instance behaviour plays an important part in determining the level at which the population is limited. Not only is density-induced mortality indirectly due to the habit of the larvae of biting any others with which they come into contact; but the adults intensify larval crowding by congregating in particular parts of the environment for egg-laying, although there are many other places in the vicinity which appear to be equally suitable for oviposition. In this way. *A. howitti* tends to limit its abundance far below the level which the resources of the environment could maintain.

Unusual and very important evidence of population self-regulation is provided by the field data concerning *Thrips imaginis* Bagnall recorded by Davidson and Andrewartha (5), and also by their statistical analysis of these. They made daily records of the numbers of adult *T. imaginis* found in 20 blooms of selected types of roses over a period of 14 years. Using the method of partial regression, they studied the degree of association between temperature and rainfall (during certain limited periods) and the numbers of thrips recorded. They obtained closest correspondence between observed and calculated thrips numbers each year when they studied the mean of the numbers of thrips observed each day during the 30 days preceding the annual peaks.

The equation used to calculate these "peak numbers" is given by Andrewartha & Birch (1, p. 579) in the logarithmic form, which is convenient for computation; but for the study of its biological implications it is more convenient to use the equivalent nonlogarithmic equation, which is:

$$Y = \overline{Y} \cdot a_1^{(x_1-\bar{x}_1)} \cdot a_2^{(x_2-\bar{x}_2)} \cdot a_3^{(x_3-\bar{x}_3)} \cdot a_4^{(x_4-\bar{x}_4)}$$

where Y represents "peak numbers"; $x_1 \cdots x_4$ represent meteorological factors, recorded in day-degrees, or inches rainfall; $a_1 \cdots a_4$ are the antilogarithms of the regression coefficients in the logarithmic equation; and a bar shows that the term below it is a mean.

This equation may be expressed verbally thus:

"Peak numbers" in given year = Mean "peak numbers" × Terms representing the departure in the given year of the influence of each weather factor from its average observed influence.

Andrewartha & Birch (1, p. 578) rightly stress that "regression measures degree of association; causal relationships need to be inferred on biological grounds." Let us apply this dictum to the equation.

The only pertinent direct effects temperature and rainfall can produce upon thrips are variations in their ability to survive and reproduce. If, therefore, thrips numbers were directly determined by weather, the number existing at any given time would be the historical resultant of weather-induced changes in number. So, an equation describing this situation would need to contain a variable representing the historically determined number of thrips which came under the influence of the "x factors" at each period considered. However, the equation used contains no such variable, its place being taken by a constant ($\bar{Y}$). Consequently, the close association found between the "peak numbers" observed and those calculated implies that the weather-induced changes in numbers of thrips took place each year from some approximately constant number. Had the induced changes taken place each year from the number of thrips recorded during the preceding year, each observed annual "peak number" should be either higher or lower than that calculated, according to whether the preceding "peak number" was above or below the average, but there is no sign of this [see Andrewartha & Birch (1), Figure 13.06]. Note that the general level about which the numbers are calculated to vary is purely empirical, being the mean of all "peak numbers" actually observed. The data give no clue as to what determined this general level.

It is thus evident that, if the "x factors" merely induced changes in thrips numbers, some additional factor must have adjusted numbers to an approximately constant value at least once each year. Moreover, to produce such constancy, this factor must have adjusted the intensity of its action in relation to the numbers coming under its influence, for these varied greatly from year to year. In short, a density-governing factor is required to operate in this situation.

The periods when the greatest changes in thrips numbers took place were November to early December, during which time there was rapid and apparently unrestricted multiplication (culminating in the "peak numbers"), and December to the end of January, when the precipitous fall in numbers was unquestionably caused by unfavourable weather. The weather data for these two periods were neglected in the equation, each "x factor" referring to data collected during some selected fragment of the period February to October, during which numbers were relatively low and varied comparatively little in any particular year.

There is a suggestion, therefore, that the demonstrated influence of the "x factors" upon the "peak numbers" of the thrips may not have been simply the induction of changes in thrips numbers. Instead, temperature and rainfall may have influenced agents which contribute to the capacity of the environment, as Davidson and Andrewartha suggest (e.g., 5, p. 217). For example, the supply of food or of living space could be so influenced. Now, the quantity of a requisite can affect thrips numbers only when these are sufficiently high to be limited by it. This means that the numbers of thrips must be so high that the consequent depletion of the requisite increases mortality or decreases natality, at times at least. To account for the associ-

ation found between the observed and calculated annual "peak numbers," such density-governed reaction to weather-induced variations in environmental limitations must have taken place at least once a year. Presumably this happened during the relatively unfavourable period, February to October, to which the weather data used in the equation apply, the thrips being subsequently released from limitation during the favourable period, November to December, when multiplication was apparently free.

It follows that, irrespective of whether the "x factors" influenced thrips directly or indirectly, the close association found between the observed "peak numbers" and those calculated shows that some governing factor must have played an important part in the determination of the actual numbers of thrips. This cannot have been a weather factor, for such factors are inherently restricted to the legislative roles of influencing either changes in numbers or environmental favourability. The possibility that the demonstrated association could be due to pure chance appears too remote to warrant consideration.

These considerations confirm and illustrate the point I made long ago (13, pp. 133 and 176), that the existence of an evident relation between the densities of animals (as distinct from changes in density) and environmental conditions shows that populations must be in a state of balance with their environments.

It should be noted that the thrips numbers recorded do not give "a satisfactory indication of the density of the population in an area" (5, p. 222), as Davidson and Andrewartha claim they do, but this does not affect the validity of the conclusion reached. The numbers are manifestly records of flower infestations, necessarily influenced by the densities of flowers, as well as by those of thrips. The association found between calculated and observed thrips numbers implies that the flowers, like the thrips, were consistently influenced by weather conditions, as general observations indicate they are. Assuming that they were, comparison between thrips numbers at the same short seasonal period in different years would be little affected by this method of recording data, but comparison with other periods would be seriously affected because of the unrecorded, but evidently great, seasonal variation in flower density.

Although the present article is concerned only with insect populations it is important to note that the study of vertebrate populations has provided many examples of efficient compensatory reaction to even greatly changing environmental influences. [see Errington (8), and Lack (12)].

Laboratory evidence for self-regulation.—In all instances in which laboratory populations of insects have been provided with tolerable conditions (including adequate space and the replenishment of depletable requisites, such as food) it has been found that the population soon reaches a state of stability at a general level, which is related to the size of the environment provided and, particularly, to the quantity of limiting requisites present. Some populations remain fairly constant under constant conditions, whereas others oscillate in number with various degrees of violence; but each popu-

lation is stable in the sense that it continues to exist indefinitely through the operation of an innate mechanism which checks any tendency to indefinite increase or decrease. The nature of this density-governing mechanism varied considerably in the different populations studied, as is shown by the following representative examples:

Populations of *Tribolium confusum* Duval are limited predominantly by the increase of cannibalism with increasing density, but there is also a marked fall in fecundity with density [Rich (17)]. In some laboratory populations of *Lucilia cuprina* (Wiedemann) populations were limited by density-governed mortality due to competition for food, whereas in others they were limited by density-governed natality resulting from competition for adult food [Nicholson (14 and 15)]. Laboratory populations of *Callosobruchus chinensis* (Linnaeus) were found to limit themselves by direct crowding effects. Increased numbers of adults caused an increased mortality of eggs by trampling, and also a decrease in the number of eggs laid; and increased densities of young larvae caused increasing mortality as a direct effect of interference [Utida (25)].

In the cultures of *C. chinensis* into which Utida (26) introduced the parasite *Neocatolaceus mamezophagus* Ishii and Nagasawa, the beetles fluctuated in numbers continuously and rather violently for a period of 51 generations of the host, when the experiment was concluded. Utida remarks that "the mean density obtained in this experiment is not a mere mean value, and corresponds to the steady density in Nicholson's sense. An equilibrium state exists clearly in the population." His analysis showed that the beetle population was limited, not only by reaction in the intensity of attack by the parasite, but also by that of the three crowding factors already mentioned. Such sustained oscillation, resulting from the interaction of a host and parasite in the presence of additional limiting factors, illustrates the conclusion reached on theoretical grounds [Nicholson (13) Conclusion 41], that "when there is an upper limit to the density an animal may reach, interspecific oscillation may be maintained indefinitely."

Even more striking evidence of the ability of populations to adjust their densities in relation to prevailing conditions, and of the nature of the mechanisms which cause this adjustment, are provided by studies of laboratory populations of *L. cuprina* [Nicholson, (14 15, 16)], *Tribolium confusum* Duval [Watt (27)], and *Daphnia pulicaria* (Forbes) [Slobodkin and Richman (19)], in which known percentages of selected stages of the animals were destroyed deliberately. In each instance not only were the animals able to maintain themselves indefinitely in spite of this destruction (so long as it did not exceed a certain extreme value), but they also adjusted themselves about numerical levels higher than those which would be expected from the degrees of destruction imposed. In each of the numerous experiments the age-structure of the populations changed in a way which caused more individuals to reach the stage destroyed than would have done so had there been no destruction. The mechanism underlying these changes was that the intensity of interference (whether competition or cannibalism) between the

individuals automatically relaxed to a degree which exactly compensated for the imposed destruction. In *L. cuprina* [Nicholson (14, 15)] similar automatic compensatory reactions were demonstrated in populations in which fertility was lowered by subjecting them to adverse conditions.

Thus a strong tendency towards homeostasis was observed in all populations subjected to inimical factors. These populations tended to maintain constant numbers, the variations being far less than proportional to the degree of destruction or reduction in fertility. Under certain conditions, in *L. cuprina* there was an "over-compensation," the population level of adults being increased by the operation of an inimical factor.

Deductive evidence for self-regulation.—Apart from evidence available to us from the deliberate field observations, or from laboratory experiments, we possess certain knowledge of populations derived from the common experience of large numbers of people who were not necessarily concerned with this subject at all.

For example, experience has shown that it is not sufficient merely to reduce an insect pest to a very low level by a single application of an insecticide in order to control it. On the contrary, to keep pests under control, we must continue to apply insecticides at frequent intervals indefinitely. In the absence of insecticides the mortality and natality of any pest necessarily must be approximately equal; but this must also be true when pests are held in control by insecticide, for in both situations the pest does not increase, nor does it decrease progressively. It is evident, therefore, that the application of insecticides causes relaxation in the operation of some natural check, which is demonstrated by the well-known fact that pests increase in abundance rapidly for a time when chemical control is discontinued. This acquired ability to multiply is often due to direct destruction by the insecticides of natural enemies which had previously held the pest in check; or to indirect reduction of these enemies because of increased difficulty in finding their food, the pests. This ability of pests to return towards, and even to swing beyond, the original degree of abundance when the use of insecticides is discontinued is unfortunately an undeniable characteristic of chemical control. There seems no possible explanation other than that reduction in density has relaxed the intensity of density-induced resistance to multiplication. Insecticides generally function purely as powerful legislative factors; but if they are applied only when the pests are considered to be too abundant, their application is a governing factor.

Logical argument based upon certain irrefutable facts shows, not merely that populations may regulate themselves by density-induced resistance to multiplication, but that this mechanism is essential [Nicholson (15, p. 59)]. Fundamental characteristics of all organisms are: they cannot persist and reproduce unless all conditions are favourable; they inevitably multiply when conditions are favourable; and they inevitably deplete the limited supplies of some of their requisites, notably food, to provide for growth, reproduction, and activity. Consequently, if multiplication is not first arrested by "something else," populations inevitably increase until they limit them-

selves by depleting some essential requisite to the lowest level they can tolerate permanently. Note that the limiting requisite could be space tolerably free from enemies, or harmful metabolites. Also, the limits of toleration are often determined by behavioural reactions before there is an actual lack of any requisite.

If this "something else" is "density-dependent," it becomes an agent of self-regulation: so let us assume for the moment that it is density-independent. There are several possibilities. (*a*) If it is temporary in operation the population will multiply once more as soon as it relaxes its influence, until ultimately density-induced resistance prevents further increase. (*b*) If it is permanent in its operation and renders the environment unfavourable, then the population will dwindle to extinction. (*c*) If it is permanent and just sufficient to prevent further multiplication, there are two possibilities. (*i*) The "something else" may itself be just sufficient to prevent multiplication, so limiting the density of the animals to levels below the threshold density at which environmental depletion begins to play a significant part. (*ii*) Alternatively, it may arrest population growth by adding its resistance (which alone is insufficient to counteract multiplication) to the resistance induced by the population.

These are the only situations in which the species is able to persist, and it will be noted that in all of them the adjustment of the population level in relation to environmental conditions is carried out by density-induced reaction; although nonreactive factors may play an important part by influencing the levels at which populations are so adjusted. Thus, it seems impossible to conceive of any situation in which populations do not adjust their densities in relation to the environmental conditions by themselves inducing a change in resistance to multiplication, when their densities are inappropriate to the prevailing conditions. This is the basic justification for the belief that all persistent populations exist in a state of balance in their environments; for "balance" refers to such a condition of corrective reaction to change which holds a system in being.

Criticism of the Theory of Self-Regulation by Populations

In a recent *Review* article Thompson (23) has presented all the arguments he could muster against the concept of density-dependence; and Andrewartha & Birch (1) have made such criticisms the dominant theme almost throughout their book. Consequently, although many biologists have expressed doubts about the importance, or even the existence of density-dependence, these objections are covered by the two works just mentioned; and it is convenient in this short discussion to refer almost exclusively to them. The reader of these two publications soon realizes that the basic arguments used are few, these being reiterated frequently in different guises and combinations. I therefore propose to crystallize out and to consider the basic objections made—ignoring the numerous minor and irrelevant issues raised. While fully recognizing that I share the theory and concepts criticized with many other ecologists, I feel honoured that my investigations

and conclusions should have been selected by these authors as the main targets of criticism; for I firmly believe they represent the truth, and provide a reliable base from which new advances can be made towards the goal of a thorough understanding of how populations are regulated in nature.

Andrewartha & Birch (1, p. 19) quote Elton (7) as saying, "it is becoming increasingly understood by population ecologists that the control of populations . . . is brought about by density-dependent factors." They comment,

> when we search the literature for the evidence on which this "understanding" is based, we find that it is not really a *conclusion* based on scientific experiment but rather that it has more of the status of a *dogma*. It has come to be accepted because it has been asserted strongly by a number of authors.

This is a surprising statement when one considers that most of the evidence for the operation of density-dependent factors which has already been given in this article has been readily available for many years.

On page 583 the same authors say that

> the dogma of "density-dependent factors" is unrealistic on at least two major counts: It ignores the fluctuations of r with time, which may be induced by seasonal and other fluctuations in the components of environment; it also ignores the heterogeneity of the places where animals may live.

The first of these criticisms is quite untrue, for r simply represents the ability of an animal to multiply under given conditions, and the same factor appears in the equations of Lotka, Volterra, Nicholson and Bailey, and others, although different symbols are used there. It is clear from these equations that if the value of r varies in space or in time this will vary the levels which the animals attain, or oscillate about. Thus, these equations and analogous discussions indicate what would happen when r is influenced by the heterogeneity of the places where animals may live. However, although the heterogeneity of the environment is often referred to [e.g. Nicholson (15, p. 46)] in discussions concerning the self-regulation of populations, it is merely regarded as one form of variation in the influence of legislative factors which plays a part in determining population densities. It is not regarded as an integral part of the governing mechanism of populations, for, as will be shown shortly, it cannot play the decisive role attributed to it by the authors quoted, and some others, notably Thompson (23).

Andrewartha & Birch (1, p. 17) say

> the additional idea that Smith combined with Chapman's "environmental resistance" was the assumption that the "density-dependent" component of "environmental resistance" influences mortality in direct proportion to the density of the population. The objections to this are twofold: it is unlikely that "density dependent" components do act in this way, and, in the second place, the division of environment into "density-dependent" and "density-independent" factors is misleading because all the evidence indicates that there is no component of environment such that its influence is likely to be independent of the density of the population.

As to the first objection it is true that, in the simplified symbolic nota-

tion used by Smith, mortality due to the density-dependent component is directly proportional to the density of the population, but this direct relation is not an essential part of the theory of density-dependent reaction. In fact, in the equations used by Lotka, Volterra, Bailey ,and others this direct linear relationship does not exist; nor is any such direct relationship assumed in nonmathematical discussions of the same problem. This then, is not a valid criticism of the general hypothesis.

In justification of their second objection these authors (p. 18) say

> it is difficult to imagine an area so uniform that all the places where animals may live provide equal protection from the elements, and it is certain that the proportion of animals living in more favourable places would vary with the density of the population. A smaller number is likely to be better protected than a large number in the same area.

This intuitive conclusion is almost certainly correct; but the implication that the inimical elements may be regarded as density-dependent factors is untrue, for they are quite uninfluenced by the density of the animals. Their effect upon the animals is certainly intensified with increasing density, but this is only because competition for shelter exposes a higher proportion of the animals to them. The density-dependent factor is the availability of unoccupied shelter, and not the inimical element.

A very strange additional argument is put forward by Andrewartha & Birch (1, p. 18) in support of their second objection quoted above. They consider large and small populations of animals exposed to frost which kills some of them, and argue that the fraction so killed may be different in a large population from that in any given small population. This is true, for small samples are seldom completely representative of the large populations from which they have been taken. On the other hand, if we consider a single very large population and a large number of small populations which together equal the large population in numbers, there should be no significant difference between mortality in the two groups. This statistical variability associated with size of population has nothing whatever to do with density-dependence, as the authors imply.

To support their contention that there is no need for density-dependent factors to regulate natural populations, Andrewartha & Birch (1, Ch. 13) briefly describe the results of studies on a number of populations of different kinds of animals in which they claim that no evidence was found of the presence of density-dependent factors. Apart from the fact that all these studies are incomplete, and that consequently there is a possibility that density-dependent factors have been overlooked, even the abbreviated descriptions given by these authors indicate the presence of factors which may well be density-dependent in some of their examples—as Solomon (20) has already shown in some detail in his criticism of their discussion concerning the population of *Austroicetes cruciata* Saussure studied by Andrewartha.

A disadvantage of this method of argument is that inability to find a density-dependent factor does not prove its absence, unless it is found possible to account for the regulation of the population completely in terms of

factors of other kinds. Such complete knowledge has not yet been achieved for any field population. Even should it be proved, however, that no density-dependent factor operates against populations of a given kind of animal in a given situation, this would not necessarily be inconsistent with the generalization that density-dependent reaction is necessary to adjust populations to their environments. This is because, as has already been shown, density-dependent reaction must necessarily cease to operate at the limits of distribution of a species in a graded environment.

Referring to the investigation of *Thrips imaginis* Bagnall by Davidson & Andrewartha (5), Andrewartha & Birch (1, p. 582) claim that "not only did we fail to find a 'density-dependent factor,' but we also showed that there was no room for one." They consider that weather alone controlled this population. I have already shown that the equation upon which these claims are based "explains" only the observed variation in numbers from year to year: it gives no clue as to why the actual level about which this variation took place had the value observed. Consequently, as it is the special characteristic of a "density-dependent factor" that it adjusts population densities (i.e. actual numbers), there most certainly is room for one in the control of *T. imaginis* populations. The data and statistical analysis described by Davidson & Andrewartha clearly imply (see p. 112 of this article) that such a factor must have operated to produce the population events they describe: the quoted claim is a *non sequitur*, being inconsistent with their data and analysis.

Thompson's criticisms and arguments are in general very similar to those made by Andrewartha & Birch. It is true he does not speak of the "density-dependent dogma" but it would seem that he views the related concept of "balance" in this light. Thus he says (23, p. 384),

> As Nicholson has said his method is primarily deductive. Nevertheless it is based upon an induction or in other words it starts with a proposition which expresses, in the opinion of Nicholson, a natural fact. This proposition is that populations exist in a state of balance. In the discussion of Nicholson's views published in 1939 I expressed the opinion that this was his fundamental thesis. He has not objected to this view, and his most recent paper indicates clearly that it is correct.

It is true that I have not modified my views about balance in my recent publications; but it is not true that the existence of balance is my fundamental thesis, in the implied sense of a gratuitous initial postulate. That populations exist in a state of balance with their environments is a conclusion, not a primary postulate.

Arguing against the concept of balance Thompson (23, p. 385), starting with my statement that without balance "the population densities of animals would be indeterminate and so could not bear a relation to anything," arrives at the surprising conclusion that

> in this argument the concept, "in the state of balance" is the exact equivalent of the concept "caused." Nicholson is therefore simply saying that populations are what they are because things are what they are.

Now, in the sentence which preceded the one which Thompson quoted, it was the evident *relation* between population densities and environmental conditions which I stressed, and not simply that the population densities need to be accounted for. My argument is that this relation between population densities and the favourability of their environments can be maintained only by a mechanism which tends to correct any departures from it; and such a mechanism can counteract departures only if its action is influenced by them.

Thompson (23, p. 381) purports to present my viewpoint when he says

> that although the results of observation may be used to illustrate and to convince the doubters, they are not really needed to give us information about what is happening in nature. This can be deduced with incontrovertible certainty from the incontrovertible premises adopted.

Now, my primary premises are facts, such as that all kinds of animals multiply when living under favourable conditions, and that supplies of requisites are limited and tend to be depleted as the animals increase in number. Logical deduction from such well-established facts leads to the conclusion that, to persist, populations must exist in a state of balance, this being responsive to both population and environmental change. As this conclusion is consistent with all known facts concerning populations and inconsistent with none, one may legitimately regard it as forming part of a sound general theory of population regulation. Like any other conclusion, however, this needs to be checked and rechecked by reference to populations of different kinds existing under different conditions. Such checking by observation and experiment is required, not merely to prove or disprove the primary conclusions, but also to provide new information, so extending our knowledge of population regulation.

Thompson (23) also objects to my concept of "populations." On page 391 he says

> The population is referred to as if it were an entity, but as an entity it exists only in the mind, having merely the status of a concept. Nicholson has reified or hypostatized it and has thus created a quite unreal being to which he then ascribes the power of self-preservation or adaptation. By such misleading language the reader is led to regard self-regulation as a fundamental property of populations. In fact, however, the only real beings that exist in the real world are individual organisms, and they alone (if we except the animal societies) have the power of self-regulation or adaptation.

Now the presence of other individuals of the same species in the neighbourhood of a given animal is one of the most potent factors in the environment of the individual. It is therefore quite absurd to claim, as Thompson does, that a population is simply an arbitrary collection of individuals which behave quite independently. Thompson carries this idea to an extreme by describing how unpredictable may be the fate of 20 caterpillers (p. 391) or 10 cows (p. 392) when one considers the possible devastating effects of purely haphazard events upon such so-called "populations." Thompson (p. 391–

92) says "carried to this extreme, the conception (of self-regulation) assumes a slightly comic aspect; nevertheless we have arrived at this point simply by following the principles to their logical conclusion." I agree about the comic aspect, which is supplied by Thompson, but dispute the logic of his argument.

Thompson is critical of my conclusion that, when assessing the relative importance of the various factors in controlling populations, no reliance can be placed upon the percentage of animals destroyed by each. He comments (p. 394),

> But what this means is, that the factual evidence we can obtain at any particular moment in nature, has not necessarily any significance in regard to the problem we are trying to solve. To discover the inner meaning of the facts a very lengthy and arduous investigation has to be made. In cases where this investigation has not been made, we simply have to rely on faith: "the substance of things hoped for, evidence of things unseen," as St. Paul says.

The first part of this comment implies that the only field evidence we can expect to obtain is that concerning percentage mortality. The second suggests that lengthy and arduous investigations are not to be tolerated, even to obtain truth. The last part is a gross misrepresentation. I simply maintain that if a population is persistent it is logical to believe that a governing factor is operative and to search for it, not as a matter of faith, but because logical deductive reasoning from well established facts clearly implies that such a factor must exist.

Like Andrewartha & Birch, and many other authors, Thompson places great stress upon the fact that many animals, notably herbivores, consistently remain at population levels far below those which apparently could be supported by the available food supply. He rightly points out that I do so myself, but he grossly misquotes (23, p. 393) the pertinent passage (Nicholson, 15, p. 49). The passage itself reads

> Almost all kinds of plants are attacked by one or more species of animal, and animals tend to reduce their food supplies to the threshold density at which they can barely find enough food to maintain themselves and to produce sufficient offspring to replace them at death. With most kinds of herbivorous animals this would lead to an extremely sparse distribution of their food plants—yet observation indicates that terrestrial plants succeed in occupying fully practically every site in which conditions are suitable for plant growth. The question is, how can these apparently contradictory conclusions be reconciled?

I follow this query by citing ways in which the natural enemies of herbivores may prevent these eating out their food plants and conclude, (p. 50)

> probably many factors other than the availability of their food plants and the attack of natural enemies limit the populations of some plant eating animals, but there seems very little doubt that the major influence which prevents animals reducing vegetation on the earth to extreme sparseness is the attack of phytophagous animals by enemies of their own.

Thompson comments (23, p. 394)

These remarks, if I interpret them correctly, constitute an acknowledgment that the insect enemies of plants do not usually appear to be depleting and impairing essential things to the threshold of favourability, for the plant food is assuredly a "requisite" for the phytophagous insect.

This statement reveals confusion of thought, for the food plant is by no means the only requisite for the phytophagous insect. A basic concept of the theory of density-governing reaction is that populations are limited by the first factor, or group of factors, which a growing population reduces to the lower limit of favourability for the animals concerned. In the situation under discussion the parasites of the phytophagous insects reduce their own food supply, the phytophagous insects, to the threshold density, this being the density-governed reaction which limits their own numbers; or, looking at the situation in another way, the phytophagous insects are limited, not by depleting their own food supply, but as the food supply of their enemies. Thompson's (23, p. 394) statement that the threshold level for the parasite is "a level below which the extinction of both the phytophagous insect and its insect enemy would occur" is incorrect. When the phytophagous insects are below this level, the parasites are caused to decrease in number and, in consequence, more hosts are permitted to survive in the next generation, so ultimately ensuring a supply of hosts adequate to prevent the extinction of the parasites.

On page 398 Thompson (23) makes the strange statement that "Nicholson does not deny that density-independent factors have a determining influence on density." The correct statement is that I have asserted this fact categorically on numerous occasions. The following conclusions in my 1933 paper (13) are pertinent—

C 67. The distribution and densities of all animals are ultimately dependent upon the physical environment.

C 68. Physical factors that are uninfluenced by the densities of animals cannot directly determine these densities.

C 69. Physical factors may indirectly influence the densities of animals by modifying the positions at which other factors produce balance between animals and their environments.

C 70. The destructive action of physical factors may either increase or decrease the steady densities of animals.

Suggested Alternative Mechanisms Of Population Regulation

Various suggestions have been made by many authors as to how animal numbers may be regulated in nature. Andrewartha & Birch (1) and Thompson (23) have repeated many of these, and at times have modified them a little, in support of their contention that balance and its mechanism of density-governed reaction are not essential in population regulation. Although many suggestions have been made, it is found that these fall into a few easily-recognizable groups which can be regarded as distinct hypotheses. I have coined names for these and will now deal with them briefly in turn.

The "limited resources hypothesis" of population regulation.—After considering a hypothetical example of bees hunting for augur holes in which to make their nests, and making the tacit assumption that the bees experience no difficulty in finding these nesting sites, Andrewartha & Birch (1, p. 24) state that this example

> is sufficiently close to nature to illustrate quite nicely the principle that when the supply of some necessary resource is inadequate for the number of animals present, it is the quantity of the limited resource which determines the density of the population, not the intensity of competition.

If it were true that this situation is sufficiently near to nature to represent the normal mechanism of population control, I would agree that it is unnecessary to speak of competition as the cause of population adjustment, although it operates even in this excessively simple situation. Here, however, it is simply the mechanism which denies the surplus individuals access to nesting sites; it determines which, and not how many, animals are successful.

This idea that each favourable environment has a definite capacity for animals of a given type, which is proportional to the level of the environmental resources and inversely proportional to the demands made upon these by the individual animals, has been expressed by many authors. It is, for example, one of the two basic premises of the Verhulst-Pearl logistic equation, and the same idea is used in other mathematical equations. There appears to be a tacit but illogical assumption that, as there must be a limit to the size of a population any limited environment can support, therefore this size is determined by the environmental capacity alone. This assumption has been proved to be invalid by many field observations and laboratory experiments with populations. These show that, quite apart from the demands the individual animals make upon the resources, animals greatly influence the population levels they can attain by their characteristic activities and behaviour. Very briefly I will mention some of these.

The simple situation postulated by Andrewartha & Birch is probably most closely approached by birds and certain other animals which have the territorial habit. The behavioural responses of the individuals of each such species tend to restrict each territory to a particular size, and there is necessarily room for only a certain limited number of territories in any particular favourable region. When, as usually happens, there are too many individuals to be accommodated in the space available, active competition drives the surplus animals into fringing country, so that the population of "landed proprietors" tends to be restricted to a particular number. Even so, the total population is variable because there are generally numerous surplus individuals, many of which manage to survive in spite of inability to obtain territories. Usually these surplus individuals fail to produce offspring. But the territorial habit is not as inflexible as is sometimes supposed, there often being a considerable variation in the size of territories which is associated with the pressure of the population seeking territories.

Andrewartha & Birch recognize that populations of many kinds of animals do not approach their first hypothetical situation as closely as those of species which limit themselves by territorial behaviour. They describe (1, p. 498) how, with increasing populations of blowflies, there is an increase in the amount of food eaten which may be said to have been "wasted," in the sense that it is consumed by individuals which die before reaching maturity. They criticise the idea that reduction of the emerging flies far below the maximum number which the food could support is due to competition, preferring to say that here there has been a reduction in "effective" food. This concept of "effective food" is not an alternative to that of competition: it is not in itself a mechanism, but merely an important resultant of competition. They also annunciate (p. 500) "the general ecological principle" that "when the food is a living plant, the size of the *total stock of food* depends upon the number of animals feeding on it. . . ." This dependence is also a resultant of density-induced reaction: it is simply an observation, and not an alternative mechanism.

It is thus evident that populations generally are not directly limited by the resources of their environments, but are limited in relation to these by density-governed reactions which commonly have the underlying mechanism of competition. This mechanism often holds populations far below the apparent capacities of their environments, as indicated by the abundance of resources, (see p. 109–10) and often imposes characteristic patterns of population change which may be associated with, or unrelated to, environmental changes.

The "diffusion hypothesis" of population regulation.—Thompson (22, p. 338) says

> it is clear that though spread from a centre will probably entail some movement inward as well as outward, the proportion of individuals outside the favourable zone will become progressively greater, generation by generation. *To the extent that this occurs, environmental factors in general are working so as to produce the effect of density dependent factors, as the organisms spread in space, though no true competition may be involved.* (Thompson's Italics.)

He repeats this general idea in many places in his publications, but at no time does he give any factual evidence to support it, and he makes only one attempt to show how such diffusion could possibly limit populations. To illustrate his contention he constructed a hypothetical example (22, p. 339) and, using arithmetical considerations, showed that, under the postulated conditions, the fraction of a population destroyed by exposure to adverse conditions would increase progressively with time. He apparently failed to notice, however, that his equations also showed that the number of *survivors* would increase rapidly from generation to generation to indefinitely large numbers. Thus the number of surviving offspring in the first, second, and eighth generation respectively are $8d$, $36d^2$, and $3435d^8$, where d is the number of eggs deposited each day in the first generation. Thus Thompson's hypothetical example leads to a conclusion diametrically

opposed to his own tenets. The diffusion hypothesis does not warrant serious consideration unless someone can at least show that it conceivably could lead to population limitation.

There is a widespread appreciation of the fact that progressive growth of populations may at times be prevented by animals leaving overcrowded areas and entering intrinsically less favourable areas. This however, is by no means the view that Thompson appears to hold, for competition is here the key mechanism. As I have previously stated (13, p. 173)

> migration, provided it is dependent upon the severity of competition, may control the densities of animals against which physical factors alone operate. Competition forces the surplus animals into unsuitable portions of the environment, where they are destroyed by the physical factors.

The "chaos hypothesis" of population regulation.—Thompson (23, p. 398) says "in my 1939 paper I said that the discontinuity and variability in habitats produced by the physical factors is undoubtedly the primary extrinsic factor of natural control." Similarly at the bottom of page 399 he stresses the importance to organisms of haphazard changes in their environments, and continues on page 400

> such changes are continuous and of tremendous complexity. Their existence, which is one of the most obvious facts of nature, makes it quite superfluous to postulate for the control of organisms such so-called reactive factors as natural enemies and the depletion of the food supply.

Andrewartha & Birch express the same idea (1, p. 21)

> it is precisely because change is the general rule in nature that there is no need to invoke "density dependent factors" to explain the mean numbers in a natural population or the fluctuations that occur from time to time.

These authors support this strange contention by reiteration alone. They appear to consider it self-evident that, if populations are continually increasing and decreasing owing to the buffeting they receive in their environments, this is sufficient to maintain them in being. The vague, but unsound, background idea is apparently that, if a particular population is decreasing, changing conditions will cause it sooner or later to increase again. Now, in the postulated absence of density-induced corrective reaction, if the conditions were more often favourable than unfavourable, the population would inevitably increase in time without limit; and if more often unfavourable, it would decrease eventually to zero—the progressive change doubtless being erratic.

Thompson attempts to counter this argument against the "chaos hypothesis" by pointing out that animals sometimes do increase to very great numbers, and that species do become extinct. Thus he says (23, p. 401)

> in extreme cases, where a chance conjunction of favourable circumstances has led to long continued increase, the induced shortage of requisites or the multiplication of

natural enemies drawn in by the mass attraction of the host population, may reduce this population; but such cases are clearly exceptional.

Thus he admits density-induced governing reaction as an exception but gives no factual evidence to support his contention that it is exceptional. On page 382 he says

some species go on increasing for long periods of years. Others in consequence of environmental changes producing conditions with which they cannot cope, decrease in numbers and disappear completely. Numberless catastrophes of this kind have occurred in the past and though the majority of them escape notice, still continue to occur.

Andrewartha & Birch (1, pp. 663–665) also stress the fact that innumerable species have become extinct in the past and that extinction still occurs, particularly in local populations; but these facts do not support their contention, as they seem to believe, that populations can generally continue to exist without the aid of density-governing reaction.

These authors evidently do not appreciate the explosive characteristic of multiplication which, in the absence of induced opposing reaction to change, would cause populations either to reach vast numbers, or to be reduced to extinction, in a very short time when their properties even slightly exceed, or slightly fall short of, those necessary to balance the average properties of their environments. For example, if a species which can multiply at the rate of 100 times per generation when unrestricted is subjected to 99.5 per cent destruction, its numbers will be halved; whereas, if the destruction is 98 per cent, the numbers will double in each successive generation. Such geometric progressions produce vast effects in a very short time, yet only a small change in the general favourability of the environment is necessary to change from one situation to the other; and much smaller changes would produce similar effects in only slightly longer times.

The "environmental-fit hypothesis" of population regulation.—Thompson (23, p. 399) says

The Darwinian geneticists claim that every single specific characteristic of an organism is positively adaptive. The organism is therefore fitted to the environment, as Fisher has said, like a complicated key to the lock.

It is my impression that Thompson's arguments are largely based upon the tacit assumption of the truth of this idea that organisms have developed properties which make them precisely fit their environments. This idea appears to be very widespread, although it is seldom explicitly stated, and it is generally assumed that natural selection is the mechanism which brings about this "fit" and which, at the same time, regulates populations.

Natural selection could not possibly bring about this state of qualitative balance between animals and their environments, for to do so it would be required to favour less potent individuals at the expense of more potent ones when the properties of the latter were better than needed and so tended to

cause the population to increase progressively. Moreover, even if qualitative balance could be produced it could not regulate populations even in constant environments for, without the intervention of other factors, this balance would be maintained at any population level. In addition, the concept is irreconcilable with field observations, for it is well known that most species can survive and maintain their numbers in environments which differ considerably from one another. The properties of a species cannot very well be adjusted precisely to each of a number of widely different environments.

The concept of qualitative balance appears to underlie Chapman's well-known theory of "biotic potential." Thus he says (3, p. 183)

> nature has required that organisms which live in environments that offer great resistance, possess a high biotic potential in order that, after all the resistance of nature has been met, there may still be survivors to maintain the population. . . . The fact that our present fauna has survived down through the ages is evidence that biotic potential and environmental resistance have tended to maintain a balance.

Throughout his arguments there is frequent reference to the adjustment of biotic potential to the resistance of the environment, but I can see no justification for the view of some biologists that Chapman included density-induced resistance in his concept.

The "intrinsic limitation hypothesis" of population regulation.—Thompson (23, p. 383) makes the following assertions:

> The fact that there are species, that is, a variety of essentially limited things, means that their ability to increase is necessarily limited. . . . When we recognize the specific intrinsic limitations of organisms we have, in my opinion, arrived at the absolutely fundamental explanation of natural control: that is to say, the fundamental explanation of the fact that no organism increases without limit. This is a philosophical explanation, which indeed verges on the metaphysical, and this I think is a sign that we have really got to the bottom of the subject.

This does not make sense, for species are concepts limited alone by the characters we used to define them, whereas species populations are inherently capable of unlimited growth, for all animals continue to multiply so long as conditions remain favourable.

The Andrewartha-Birch theory of population regulation.—Andrewartha & Birch (1, p. 648) head Chapter 14 of their book "A General Theory of the Numbers of Animals in Natural Populations," and they begin it by saying, "in this chapter we will have to build a general theory about the distribution and numbers of animals in nature." The method they used to build their theory is naïve, and the statement of their "general conclusion" which appears on pages 660–661 lacks the qualities of a "general theory" in the scientific sense for, although the constituent statements are consistent with certain facts known about populations, they do not individually, or collectively, account for the regulation of "the numbers of animals in natural populations."

Throughout their book these authors persistently emphasise the im-

portance of establishing facts by observation when seeking an explanation of the regulation of natural populations. They are critical of the use of mathematical models and say (p. 11)

> ecologists, and especially mathematicians with a slight knowledge of biology, seem to be prone to the mistake of building a model with symbols which, they pretend, represent certain qualities of animals. The symbols are then manipulated according to the rules of mathematics and, finally, the conclusions are translated into words which purport to describe some law of biology. This is a tricky game. Animals are too complex to be represented by symbols. The conclusions derived from such models can, at best, have a very limited scope; at their worst they may be grossly misleading.

In view of these strictures, one is surprised to find that their "general theory" depends for its support almost entirely upon pictorial models which are much cruder and more over-simplified than the mathematical models they criticised. The device is one of which Thompson also makes much use. It consists of first visualising a picture of a hypothetical "population"—which is not a true population of animals forming a coherent whole, but is merely a fragment of such a population. The hypothetical individuals are assigned certain properties and certain conditions to live under; then, with little, if any, logical argument, a second picture is imagined which is supposed to represent the outcome of the first hypothetical situation. The reader is presumably expected to accept this second picture as a proof of the author's contentions.

In general, the pictured results are plausible enough, but unconvincing because of the lack of factual and logical support: one could readily, and plausibly, visualise other results which are not consistent with the author's tenets.

This pictorial method of argument is necessarily restricted to producing as conclusions those which were preconceived by the author: it is merely illustration, not argument. With this method mistakes can be made both in formulating the problem and in reaching conclusions; whereas with the method of mathematical models the results can be relied upon absolutely, provided the mathematical formulation is appropriate.

Andrewartha & Birch (1, p. 660) reach the "general conclusion" that

> the numbers of animals in a natural population may be limited in three ways: (*a*) by shortage of material resources, such as food, places in which to make nests, etc.; (*b*) by inaccessibility of these material resources relative to the animals' capacities for dispersal and searching; and (*c*) by shortage of time when the rate of increase r is positive. Of these three ways, the first is probably the least, and the last is probably the most, important in nature.

Item (*a*) has already been discussed in the section dealing with the "limited resources hypothesis" of population regulation. Although limited resources play an outstandingly important legislative role, they do not themselves determine population levels; they do so only through the medium of density-governed reaction, which often limits populations far below the

levels apparently permitted by the environmental resources, and which may greatly influence the pattern of population change.

As to item (*b*), inaccessibility of material resources cannot itself limit populations. If the degree of inaccessibility is such that animals find insufficient to maintain themselves and to produce offspring at the replacement rate, the species cannot exist; whereas, if the resources are not so inaccessible, the population is permitted to increase progressively until, as I concluded long ago, [Nicholson (13, p. 168)] "before all suitable locations are occupied, the densities of animals are limited by difficulty in finding unoccupied ones." The mechanism is that competition for material resources, in all situations, tends to reduce the availability of still unused resources to the minimum the animals can tolerate permanently; and so the greater the degree of dispersal, and the lower the capacity of the animals for searching, the larger is the fraction of resources remaining unused at all times in the steady state.

The situation implied by item (*c*) is very common in temperate and subtropical regions, in which unfavourable periods of cold or dryness are regularly followed by favourable periods of warmth or moisture. It is assumed that a population is reduced to so low a level during an unfavourable period that multiplication is unrestricted by the limitation of environmental resources during the following favourable period. Consequently we may reasonably substitute the "innate capacity for increase" (r_m) for the term r, and represent the increase of a population during a favourable period by the basic equation given by Andrewartha & Birch (1, p. 35) which is $N_t = N_o e^{r_m t}$. This population growth necessarily ceases when the capacity of some limiting resource is reached; but the great importance placed upon this type of sitaution by Andrewartha & Birch indicates a belief that, in general, unfavourable conditions return before the environmental capacity can be reached, so first arresting population growth and then reducing the population once more to a very low level. Now, the above equation shows that the size (N_t) of a population reached by the end of a favourable season is influenced, not only by the innate ability of the animals to multiply (r_m), and by the length (t) of the favourable season, but also by the size of the population (N_o) which survived the preceding unfavourable period. A very important question therefore is: what determines the value of N_o?

Making the assumptions implicit in Andrewartha & Birch's argument that (*a*) no limiting factor operates before the population reaches the peak numbers for the season, and (*b*) the degree of population reduction caused by the unfavourable conditions is independent of density, there are two possible situations. In the first the average, but fluctuating, severity of the unfavourable seasons over any long period of years more than counteracts population growth during the preceding favourable seasons. In this situtaion the population must follow a fluctuating course to extinction. In the second situation the severity is not so great, so in general permitting the size of the population surviving each successive unfavourable season to be somewhat greater

than that surviving the preceding unfavourable season. The value of N_o would then, in general, increase in successive seasons, until it becomes sufficiently great to permit the population to grow during the current favourable season to the level at which it causes environmental depletion to a limiting degree. This density-induced effect would prevent any further tendency for the population to go on increasing in successive years. The population would then have a seasonal fluctuation about a recognizable level such that, in general, it would grow each season to a level which caused some environmental depletion. In other words, the population would be controlled by density-induced governing reaction.

It is unrealistic, however, to assume that the reduction caused by the unfavourable seasons is necessarily independent of density. The population may well be limited during such seasons by the availability of some requisite, such as effective shelter. Competition for such limited shelter would necessarily lead to a higher mortality when the population density is high than when it is low. Such limitation during unfavourable seasons, then, might adjust N_o at so low a level that multiplication during the limited favourable periods could not cause the population to reach saturation before the onset of the next unfavourable season. The values of r_m and t are important but purely legislative factors which strongly influence the change in population densities during the favourable seasons and, by so doing, also influence the average levels of populations existing under such conditions; but competition during the unfavourable seasons is the governing influence which adjusts the level from which multiplication takes place during favourable seasons. This situation appears to be exemplified by the populations of *Thrips imaginis* studied by Davidson & Andrewartha (5).

It is clear from this analysis that the "general theory" of Andrewartha & Birch is inadequate to account for population regulation. The three ways in which they say populations may be limited are each in part true, but they are all dependent upon the agency of density-governed reaction to produce the effects attributed to them.

Thompson's "general conclusion."—Apart from conceding that, under exceptional circumstances, populations may be limited by the induced shortage of requisites, or the multiplication of natural enemies, Thompson (23, p. 401) makes only two positive statements concerning mechanisms by which populations may be regulated. He says

> If an organism does not multiply without limit this is because it is restricted by its intrinsic specific limitations in a world which is made up of an ever changing complex of other specific and limited entities. Climatic and edaphic factors are the basis of the environmental diversity, producing not only the fragmentation of habitats but a constant change in their character and location. This is the primary extrinsic factor of natural control in the sense in which I have used this expression.

That is to say, he reiterates belief in what I have referred to as the hypotheses of intrinsic limitation and of chaos, and, by implication, that of population diffusion, all of which I have shown to be untenable. For the rest he ex-

presses disbelief, in several different ways, in the ability of populations to regulate their own densities; and he asserts once more that populations are merely collections of completely independent individuals. No further comment upon these assertions is necessary.

Thompson also states that

> populations, therefore, are not truly regulated but merely vary, . . . The variation sometimes assumes a cyclical aspect, but this is usually attributable to chance, not to factors producing oscillations according to definite laws. The usual variation in the numerical value of field populations from year to year corresponds to curves based on numbers selected at random.

This appears to be a travesty of the conclusion of LaMont Cole (4, p. 22):

> it now appears to the writer that, *until definite evidence to the contrary is forthcoming*, the preferred interpretation of population cycles should be that they are essentially random fluctuations with serial correlation between the populations of successive years.

Cole drew attention to the fact that apparently cyclical fluctuations could be produced by the multi-point smoothing of random data, so drawing attention to a pitfall into which biologists may stumble, and may have stumbled already. The phrase I have italicized, however, is of great importance, but it was ignored by Thompson. The fact that "pseudo-cycles" can be produced from random data by the smoothing of curves does not throw any doubt upon the reality of definite cycles which appear when raw data are plotted without smoothing; and, in particular, there can be no doubt about the reality of the cyclic population fluctuations observed in many laboratory populations, the underlying mechanisms of which have been clearly revealed by observation. Thompson provides no evidence to support his assertion that apparently cyclic variation in populations is "usually attributable to chance."

Milne's Views on Natural Control

An article by Milne (12a) appeared while the present review was in press and I was asked to comment upon it briefly. Milne begins by discussing the theories of Thompson (1929), Nicholson (1933) and Andrewartha & Birch (1954). He gives his general approval to the first and last of these, and his restatements of them (12a, p. 195, and p. 209) merely define the "chaos hypothesis," which he adopts himself. In his view (12a, p. 212)

> The main objection to the theories of Thompson and of Andrewartha & Birch is that they either pay too little attention (Thompson) or attach no special importance (Andrewartha & Birch) to the concept of density-dependence, and so are deprived of fullness.

However, he himself considers that density-dependent reaction produces significant effects only occasionally, when numbers become exceptionally large, and he states (12a, p. 212)

the main objection to Nicholson's theory is that competing species, parasites, predators and pathogens can not control because they are *imperfectly* density dependent in action. This is at once obvious from simple mathematical and ecological considerations. It is also confirmed by the field evidence.

These considerations and evidence cannot be examined as he does not present them.

Milne presents his theory by stating that (12a, p. 209)

A *perfectly* density dependent factor will control increase of numbers endlessly, but there is only one such factor in Nature for any species. That factor, the ultimate controlling factor for increase, is the competition between its own individuals, i.e. its *own* intraspecific competition.

Then, without giving any supporting evidence, he claims that this "ultimate controlling factor for increase, intraspecific competition, is usually seldom evoked" (12a, p. 210).

Milne visualizes numbers fluctuating for long periods below the level at which intraspecific competition could operate. This view represents an unsubstantiated conclusion, for it is completely dependent upon the accuracy of his guess as to the true capacities of the environments of animals. He argues that (12a, p. 209)

Numbers increase when conditions permit and decrease when conditions so dictate. There is balance, but not between population and environment. The balance is in the environment itself. Through space and time, favourable conditions are balanced by unfavourable conditions in such a way that populations continue to exist, i.e., are controlled.

He provides no factual evidence for such qualitative environmental balance, he does not suggest any mechanism which could possibly produce or maintain it and, even if it did operate, it would not itself cause the numbers of animals to be low.

In an attempt to explain this Milne says (12a, p. 210)

What then holds numbers so far below the limit of resources for so long if not almost endlessly in so many species of insects? It seems the answer must be: the *combined* action of factors which are density independent and factors which are imperfectly density dependent, *each supplying the lack of the other.*

This could be true equally well at high as at low densities. It is merely an assertion and it explains nothing, for Milne gives no indication of a mechanism which could cause the intensity of each kind of factor to become so adjusted that it supplies "the lack of the other." He excludes the mechanism which could cause such adjustment, namely, density-induced compensatory reaction, for this adjusts populations to the capacities of their environments, not below them.

Milne concedes that occasionally numbers may become so large that intraspecific competition is induced, so preventing "collective suicide." At the other extreme he claims that (12a, p. 210)

the ultimate controlling factors for decrease in numbers are, in my opinion, the density independent factors. For, unless the latter begin at the appropriate time to favour increase instead of decrease, the remnant of individuals left by the imperfectly density dependent factors will perish.

Thus he considers that it is mere chance which prevents adverse factors from causing the extinction of species, which seems inconsistent with the claim made in the diagram illustrating his theory (12a, p. 211) that, because of density independent factors, the lower extinction level is never reached. This apparent inconsistency disappears if one is prepared to accept the "environmental-fit hypothesis" which seems to be implicit in his theory.

So far Milne's theory shows little departure from those of Thompson (23) and of Andrewartha & Birch (1). The novel feature of this theory is his concept of "imperfectly density dependent factors" which he applies to competing species, parasites, predators, and pathogens. On the grounds that the "numbers of an organism at any moment are the result of action of a complex of factors," he concludes that these environmental elements cannot control animal numbers. Illustrating this contention by reference to parasites, he argues that (12a, p. 204)

whatever response the parasite population might make to changes in the host numbers is inevitably modified by other factors . . . That is, the parasite cannot be expected to adjust its numbers, or its intensity of action, *exactly* to the host density . . .

This argument seems plausible, but it is wrong, as the following considerations show.

Let us suppose that nonreactive modifying factors directly or indirectly increase the mortality of the parasites. This would favour growth of the host population. As the hosts increase in number the chance of any parasite contacting a host necessarily improves, and so the parasite population also grows, in spite of the fact that some fraction of it is destroyed by the modifying factors. Consequently, more and more of the occupied area is effectively searched collectively by the surviving parasites, and so the fraction of the hosts attacked by the parasites increases progressively. Growth of both populations inevitably ceases when this fraction, together with that destroyed in any other way, equals the surplus fraction of host offspring.

Thus additional factors which modify numbers automatically set in train density-induced reactions. These soon compensate for the disturbance the modifying factors initially produce. The end effect is simply a change in population levels, which are not necessarily made higher by adverse factors [cf. Nicholson (13, 16); Nicholson & Bailey (16a)]. In a changing environment, this mechanism necessarily works towards the adjustment of population densities in relation to each new set of conditions.

I do not claim that density-induced reaction can compensate for the effects of all additional factors. For example, effective compensation is impossible if a nonreactive factor operates with such severity that it destroys

more than the surplus of offspring produced, or prevents the production of offspring at the replacement rate, and if it protects more than the replacement fraction of prey from attack by enemies, and also if a governing factor operates which is capable of checking enemies at a density below that necessary to control their prey.

These considerations show that additional factors may either prevent the operation of density-governing factors, or leave these completely free to adjust densities in relation to the prevailing conditions, including the additional factors—but they exercise no influence which can cause the action of the governing factors to be in any sense "imperfect." Consequently Milne's basic assumption, that additional factors necessarily prevent the action of parasites, predators, and pathogens from becoming adjusted exactly to the densities of the animals attacked, so making them incapable of controlling these animals, is wrong. It is upon this erroneous assumption that his main thesis depends.

Lack of space precludes discussion of the other illogical arguments and unsubstantiated assertions made by Milne, but this review would be incomplete if no reference were made to two of his major criticisms.

He admits that insect pests have sometimes been controlled by introducing natural enemies, but claims that "the successes, however, are not necessarily cases of an animal being controlled, *in the correct sense*, by another" (12a, p. 204), for, he adds, the evidence does not "say that the introduced parasite or predator is *alone* controlling or could *alone* control the pest at the economic or any other level" (12a, p. 204). Thus the natural enemies failed to conform to his unusual definition of a control factor: but they did respond to host densities in a density-governing way, and they did control their prey at economically tolerable levels, these levels unquestionably being influenced by other factors, notably by climate and vegetation.

Milne is highly critical of the attempts of what he calls the "Riverside School" to evaluate the role of natural enemies in control. In support of his claim that their ecological analyses are flimsy and incomplete he says (12a, p. 205)

> In the single instance where the five Riverside papers give the complete sample data in detail [DeBach (5a, Table 1)], neither the population densities ($P=0.8-0.9$) nor the degrees of leaf and twig damage ($P=0.8$) were significantly different in treated and untreated lemon tree branches. Thus the conclusions in this case were unjustified.

He evidently failed to notice DeBach's conclusion that the differences observed in this control series of observations were nonsignificant. He also overlooked DeBach's statement that these observations were made in a lemon grove where "natural enemies . . . were so scarce . . . as to be virtually non-existent" (5a, p. 585), which is repeated in substance in the heading of the table Milne criticised. Parallel tests, in which the test trees were similarly treated with low dosage DDT, were made in other places where

natural enemies were present. The nonsignificance of the differences observed in the controls showed that the great increase in scale infestation which followed application of DDT in the presence of enemies could not be due to direct effects of the insecticide, but was evidently an indirect effect produced by interference with the enemies.

It appears that Milne has read other articles equally carelessly. For example he says "I think it would be fair to say that Nicholson himself has caused confusion by misguided extrapolation from the realm of mathematics" (12a, p. 203). The theory of population balance produced by density-induced governing reaction, which I apply generally to all populations, is not dependent upon mathematical investigation, although it is illustrated by the mechanisms so revealed. The basic essentials of this theory were derived from the consideration of certain facts which appear to apply to all populations (13, pp. 132 to 140; 15, p. 59). One of the most important considerations I summarised thus (13, p. 176):

> the densities of animal populations are known to bear a relation to the environmental conditions to which they are subject, and the existence of this relation shows that populations must be in a state of balance with their environments.

Milne (12a, p. 196), by quoting the last clause of this passage alone, as though it were a complete sentence and my primary postulate, gave a spurious air of verisimilitude to the epithet "dogma" which he applies to this theory. Possibly the most significant deficiency in Milne's theory is that it is inconsistent with the relation just mentioned, and also with the orderliness we observe to underly all natural phenomena.

Conclusion

In such a short review it has naturally been impossible to deal individually with all the criticisms which have been levelled at the theory of population regulation by density-governed reaction. Basically the criticisms are few in number, but they have been repeated many times in different forms. I have discussed the essentials of all criticisms that appear to have any significance, and have failed to find even one that is valid. Suggested alternative mechanisms of population regulation also appear to be, in essentials, few in number. As I have shown few, if any, of these have any factual basis, and most of them appear to be mere guesses which are not even supported by logical argument, nor is any clear indication given as to how they could possibly work. On the other hand, there is voluminous field evidence of density-induced environmental reaction which opposes population growth with increasing intensity as populations increase in size; and there are many individual examples, both in the field and in the laboratory, of populations which undoubtedly adjusted themselves to their environments by inducing such reaction. In addition, logical deduction from certain well-established facts has shown that density-induced governing reaction

must necessarily play this role of adjustment in each persistent population. This inescapable conclusion is completely consistent with the knowledge that many factors which do not react in this way play very important parts in contributing to the determination of population levels. In brief, the theory of population balance is firmly based upon ascertained facts and logical deduction, and it is consistent with all known facts concerning animal populations.

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OVARIAN STRUCTURE AND VITELLOGENESIS IN INSECTS[1,2]

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To date, several distinct approaches to the problem of yolk synthesis have been used. The development of sectioning and staining methods resulted in a period of extensive histological investigation of the ovary. This first modern period of research on the insect ovary seems to have been initiated in 1847 by Stein (92) with his histological study of the female reproductive organs of beetles. The second major approach to insect vitellogenesis was stimulated by the appearance of special cytological methods (osmic acid methods, silver methods, Janus green staining, etc.) designed to demonstrate cytoplasmic structures such as mitochondria and Golgi apparatus. This cytological approach was avidly pursued in the second and third decades of the present century, and has continued with diminished intensity to the present time.

Recently, technological advances have become available which have made possible a new, vigorous attack on the problem of yolk synthesis in insects. The field of histochemistry has become systematized to the point where it is now a valuable research tool. Although the limitations of histochemistry have already become obvious, this discipline, which is a combination of histological procedures and analytical chemistry, shows great promise of clarifying insect vitellogenesis, especially when supplemented by biochemical and biophysical investigations. The ovaries of several insects have already been studied by histochemical methods. We can also look forward to the wider application of the electron microscope to the problem of yolk synthesis. Many of the cytologists of the preceding period believed that the various types of insect yolk were derived, by transformation, from cytoplasmic organelles; the use of ultra-thin sections studied with the electron microscope should go a long way to clarify the relationships between cytoplasmic organelles and yolk bodies. Also, very significant advances in cellular physiology have been made by biochemical analysis of isolated cellular particles; see the review by Schneider & Hogeboom (87). Among the many other tools available to the cytologist are the use of radioactive isotopes[3] and radioautography, chromatographic and electrophoretic procedures, microspectrophotometric technics, and phase-contrast, interference-contrast, and polariz-

[1] Literature survey completed in May, 1957.

[2] The following abbreviations are used in this chapter: DNA (desoxyribonucleic acid); PAS [periodic acid-Schiff (test)]; RNA (ribonucleic acid).

[3] King & Wilson (52) have calculated that 36 per cent of the phosphorus ingested daily by the adult female vinegar fly is incorporated into the eggs laid that same day. Babers *et al.* (5) have studied the effects of ingested P^{32} on ovarian fertility in house flies and roaches.

ing microscopy. Many of these methods for studying cellular form and function have been summarized in a book edited by Mellors (64).

Since we appear to be ready to embark on a new phase in the investigation of insect yolk synthesis, the time seems opportune for assembling and evaluating some of the important developments of the past. It is hoped that this review will satisfy part of this need.

The last intensive review of insect gonads was published in Schröder's *Handbuch der Entomologie* by Deegener (25) and Depdolla (26). The existence of these excellent articles, together with Gross' (33) monograph, makes it possible for me to exclude the older literature and, in general, my review will cover the subject from 1920 to the present. Occasional references to the older literature are made, however, in order to maintain historical continuity in the development of certain subjects. A complete review on the subject of insect vitellogenesis might conceivably contain a detailed description of chromosome behavior during oogenesis, an intensive review of chorion formation, and yolk resorption, and a detailed account of the embryonic and postembryonic development of the ovaries. Space requirements, however, demand restraint in the selection of subject matter and I found it necessary to bypass certain excellent papers on the reproductive system simply because they did not bear a direct relationship to the subjects I selected for discussion. The subject of endocrine regulation of the ovary is also one of great interest; since this topic has been reviewed recently by Wigglesworth (104), I will not include it in this review.

HISTOLOGY OF THE OVARY

Two main types of ovarioles are recognized in insects. Panoistic ovarioles are those which lack special nurse cells (trophocytes); the follicular epithelium is the only trophic tissue present. Meroistic ovarioles contain both follicular epithelial cells and trophocytes. Meroistic ovarioles are generally divided into two subtypes:[4] in polytrophic ovarioles, the trophocytes alternate with the oocytes in the vitellarium; in telotrophic ovarioles the trophocytes are concentrated in the germarium and are usually joined to the oocytes in the vitellarium by cytoplasmic cords.

Space limitations preclude discussion or even citation of all of the excellent papers on the histology of the insect ovary. Instead we will consider representatives of the three types of ovaries selected from the recent literature.

Panoistic Ovary

Ovaries composed of panoistic ovarioles are found in the older orders of insects such as Thysanura [Perrot (80)]; Orthoptera [Matthey (61, 62); Colombo (19)]; Isoptera [Ahrens (2); Weesner (100)]; Odonata [McGill (63)];

[4] Berlese (8) has recognized a third type of meroistic ovary, the dieroistic type, which is found in some Diptera and Hymenoptera. This atypical type of ovary consists of a sac, lacking ovariole walls, which contains a mass of follicles.

and Plecoptera [Junker (49)]. The fleas are also panoistic [Gross (34); Lass (56)] and are unique in this respect among holometabolous insects. Consult Gross (33) for a comparative account of panoistic ovaries which includes the earlier literature.

Perrot (80) has given a concise and clear account of oogenesis in the firebrat, *Thermobia domestica* (Packard). Each ovary is composed of five ovarioles. The simple ovariole of the firebrat is representative of all panoistic ovarioles with, of course, differences in detail. Figures 1 and 2 are redrawn from unlabelled figures published by Perrot. Figure 1 is a longitudinal section of the anterior end of an ovariole. The *terminal filament*[6] is a syncytial strand that performs a suspensory function. The outer surface of the ovariole is covered by a thin *outer epithelial sheath*. This sheath, in the adult, is membranous but a few compressed nuclei are visible in Figure 1. The germarial region of the ovariole contains numerous *oogonia* with an occasional oogonial cell undergoing mitosis. A short distance behind the tip of the germarium are *young oocytes;* these cells are already appreciably larger than the oogonia from which they are derived. The *primary oocytes*, near the bottom of Figure 1, have enlarged considerably but are not yet arranged in a single row. The oocytes of Figure 1 are undergoing the usual leptotene, amphitene, and pachytene stages of the prophase of the first maturation division. Scattered among the oocytes and oogonia are numerous small nuclei, the *prefollicular nuclei*. These nuclei appear to be embedded in a common cytoplasm and, at the lower end of Figure 1, the prefollicular nuclei are more uniformly oriented about the primary oocytes. I have adopted the term "prefollicular tissue" for this tissue because it is destined to form the definitive follicular epithelium of the vitellarium.

Figure 2 represents a longitudinal section of a more fully developed *primary oocyte* enclosed in a follicle of the vitellarium. A one-layered, *follicular epithelium* surrounds the oocyte. Between the successive follicles of the firebrat are the *interfollicular zones*. The tissue forming the interfollicular zones in this insect is indistinguishable from the follicular epithelium but, in more highly evolved insects, the interfollicular zone is composed of modified prefollicular tissue that is cytologically distinct from the follicular epithelium (cf. Figs. 4 and 6, *interfollicular tissue*). The vitellarium of *Thermobia* is not only covered by an outer epithelial sheath, but, in addition, a thick membrane, the *tunica*, intervenes between the follicular epithelium and the outer epithelial sheath. Perrot states that the sheath of the ovariole secretes the noncellular tunica.

Yolk is formed in the primary oocyte during the period that it resides in the vitellarium. Since nurse cells are lacking, nutritive substances from the blood are mediated only by the follicular epithelium. The term "germinal vesicle" has been applied to the oocyte nucleus in general. Often, however,

[6] Histological terms which appear on the drawings accompanying this review are italicized.

the term is restricted to the much enlarged nucleus of the primary oocyte which in insects attains its greatest size prior to yolk deposition or during vitellogenesis. In this review, I will use the term "germinal vesicle" in the restricted sense. The *germinal vesicle* illustrated in Figure 2 is in a post-pachytene phase of the first maturation division; the chromatin network is diffuse and spreads throughout the entire nucleus. A nucleolus-like mass of residual substance is also present. Later the oocyte nucleus undergoes the metaphase of the first maturation division and karyokinesis, according to Perrot, occurs in the enormous oocytes which are still in the ovariole but are ready to be ovulated. Perrot did not observe the second maturation division but we may assume that it takes place in the oocyte after ovulation.

Telotrophic Ovary

Telotrophic ovarioles are characteristic of the Hemiptera but occur in many Coleoptera. Although Deegener (25) states that the fleas have telotrophic ovarioles, specific studies of flea ovaries [Gross (34); Lass (56)] have shown that they are panoistic. Perhaps this point needs reinvestigation. An exceptional case has also been reported in the Neuroptera. Gross (34) has declared that the ovaries of *Sialis* are telotrophic but without nutritive cords; if this is true, *Sialis* is the only known non-polytrophic genus in the Neuroptera.

The hemipteran ovary has been studied by many workers. A controversy still exists as to whether some aphids are panoistic [see Uichanco (97); Hagan (35)]. The coccid, *Icerya purchasi* Maskell, is of special interest because the "females" are functional hermaphrodites; although the gonads produce both types of gametes, the female egg tubes are still clearly telotrophic [Hughes-Schrader (46)]. Recently, the structure, histochemistry and development of the ovary of the large milkweed bug, *Oncopeltus fasciatus* (Dallas), has been studied in some detail by Bonhag & Wick (14), Bonhag (11, 12), and Wick & Bonhag (101). Since this ovary is representative of the type found in many bugs, a summary of its general organization will be presented.

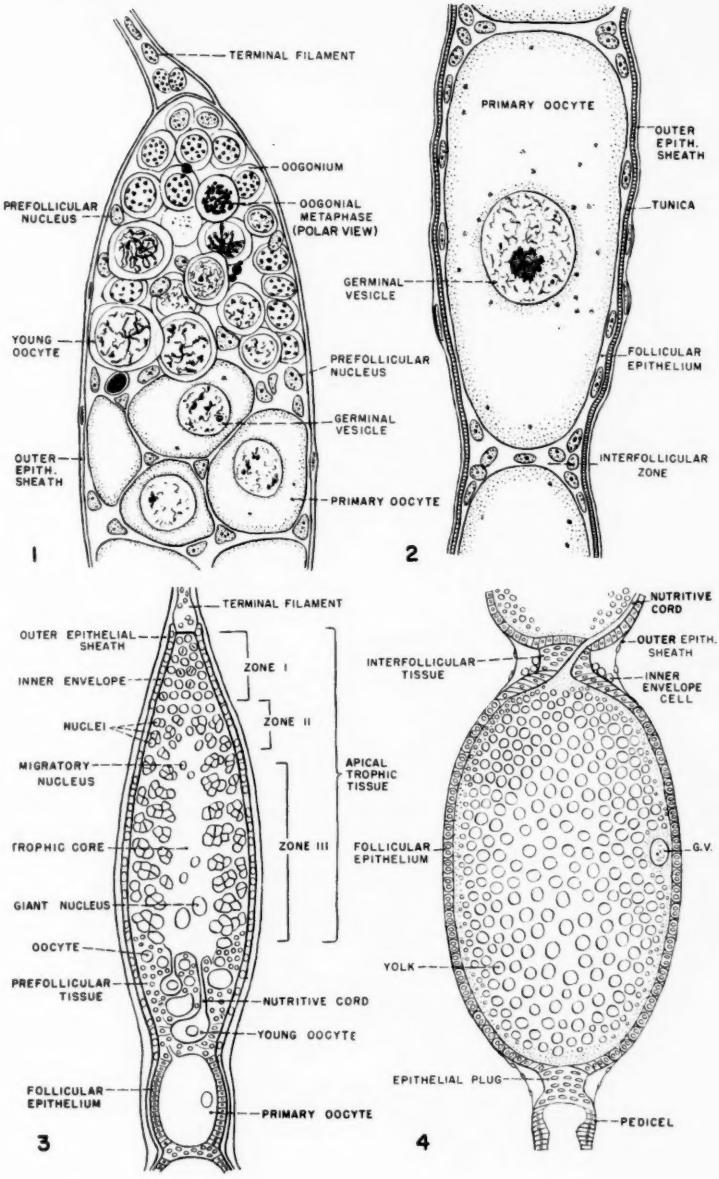
The telotrophic ovary of *Oncopeltus* consists of seven ovarioles and each ovariole comprises a terminal filament, germarium, vitellarium, and pedicel. Figure 3 represents a sagittal section of the anterior end of the adult ovariole. The long, syncytial *terminal filament* is bulbous at its posterior end. The terminal filament is cut off from the germarium by a thick, transverse septum. Two sheaths cover the ovariole, an *outer epithelial sheath* and the *inner*

Fig. 1. Sagittal section of the anterior end of an ovariole of *Thermobia domestica* [after Perrot (80)].

Fig. 2. Sagittal section of a follicle from an ovariole of *T. domestica* [after Perrot (80)].

Fig. 3. Diagram of a sagittal section of the anterior end of an adult ovariole of *Oncopeltus fasciatus*.

Fig. 4. Sagittal section of a follicle of *O. fasciatus*; the oocyte has not attained full size and the chorion has not yet been formed. *G.V.*, germinal vesicle.


TERMINAL FILAMENT
OOGONIUM
PREFOLLICULAR NUCLEUS
OOGONIAL METAPHASE (POLAR VIEW)
YOUNG OOCYTE
PREFOLLICULAR NUCLEUS
GERMINAL VESICLE
OUTER EPITH. SHEATH
PRIMARY OOCYTE
1
PRIMARY OOCYTE
OUTER EPITH. SHEATH
TUNICA
GERMINAL VESICLE
FOLLICULAR EPITHELIUM
INTERFOLLICULAR ZONE
2
TERMINAL FILAMENT
OUTER EPITHELIAL SHEATH
INNER ENVELOPE
NUCLEI
MIGRATORY NUCLEUS
TROPHIC CORE
GIANT NUCLEUS
OOCYTE
PREFOLLICULAR TISSUE
FOLLICULAR EPITHELIUM
ZONE I
ZONE II
ZONE III
APICAL TROPHIC TISSUE
NUTRITIVE CORD
YOUNG OOCYTE
PRIMARY OOCYTE
3
NUTRITIVE CORD
OUTER EPITH. SHEATH
INTERFOLLICULAR TISSUE
INNER ENVELOPE CELL
FOLLICULAR EPITHELIUM
G.V.
YOLK
EPITHELIAL PLUG
PEDICEL
4

envelope. The former is a relatively thin syncytium; the inner enevlope consists of a single layer of cells enclosed by two membranes. In the region of the large follicles (Fig. 4), the outer epithelial sheath is reduced to a thin membrane and the inner envelope is reduced to a few loose cells found mostly in the constrictions between follicles.

The lanceolate germarium (Fig. 3) is occupied largely by the *apical trophic tissue*. This tissue may be divided into three distinct zones representing three stages in the differentiation of functional nurse tissue. *Zone I* is an area of extensive mitotic activity. Cell boundaries are distinct. *Zone II* is the transitional zone of trophocyte differentiation. Cell boundaries have disappeared and the trophic nuclei have moved together to form small clusters of nuclei embedded in a common cytoplasm. A progressive increase in size of the *nuclei* from the anterior to posterior limits of *Zone II* is apparent. The nucleoli of *Zone II* are appreciably larger than those of the first zone. The nuclei of *Zone III* are disposed in the form of aggregates similar to *Zone II*, but the individual nuclei and nucleoli are much larger in the third zone. The nuclear aggregates of *Zone III* are peripherally arranged around a central cylinder of cytoplasm, the *trophic core*. Three forms of transitory nuclei are found in the trophic core: small *migratory nuclei* from *Zone II* and larger migratory nuclei from *Zone III* pass down the trophic core. *Giant nuclei* are also found in the trophic core; these are formed by the fusion of migratory nuclei. Eventually the migratory and giant nuclei break down, releasing considerable quantities of DNA into the trophic core. The possible significance of this process is discussed in a later section. The fairly rapid breakdown of nurse tissue accounts for the constant mitotic activity of Zone I during the adult life of *Oncopeltus*. Apparently mitotic divisions do not take place in the apical nurse tissues of all adult bugs [Malouf (60); Davis (24)].

The posterior end of the trophic core bears a number of cytoplasmic projections, the *nutritive cords*, which extend to the developing oocytes (Fig. 3). These cords are the bridges over which the nutritive contributions from the apical nurse tissue pass to the oocytes.

Posterior to the apical nurse tissue is a mass of *prefollicular tissue* (Fig. 3). Numerous young oocytes are found in this area. Unlike the panoistic ovary of *Thermobia*, the adult ovary of *Oncopeltus* does not contain oogonia. Wick & Bonhag (101) have shown that the oogonia produce the nurse cells and oocytes during nymphal stadia. Prefollicular tissue becomes oriented around the enlarging oocytes as they are added to the vitellarium of *Oncopeltus* but the prefollicular tissue is not depleted by this process because of its capacity to carry on mitotic activity. The more anterior follicles are lined with a columnar *follicular epithelium* (Fig. 3); later the follicular cells transform into relatively large, binucleate, rounded cells (Fig. 4) and finally become squamous.

Figure 4 is a longitudinal section of a nearly mature follicle. The *follicular epithelium* is composed of binucleate cells; the enclosed primary oocyte contains a large quantity of *yolk* and is still attached to a *nutritive cord*. The

germinal vesicle (*G.V.*) is displaced to one side and may be considered to be in a modified prophase of the first maturation division. Follicles are separated from each other by *interfollicular tissue;* this tissue represents slightly modified prefollicular tissue which became trapped between the oocytes as the latter were added to the vitellarium. The vitellarium is terminated by an *epithelial plug* which is also of prefollicular tissue origin. At the time of ovulation, the epithelial plug breaks down and the yolk-laden, chorion covered, primary oocyte enters the *pedicel.*

There is some confusion as to which of the Coleoptera have telotrophic ovarioles. Stein (92), Gross (33), and Imms (47) have stated that the Adephaga have polytrophic ovarioles and the rest of the beetles contain telotrophic ovarioles. Weber (99) and Wigglesworth (103), on the other hand, have characterized the Adephaga as having telotrophic ovarioles and the Polyphaga as having the polytrophic type. Numerous papers on the coleopteran ovary support the original view of Stein.

Scattered through the literature are reports that panoistic ovarioles occur in the Coleoptera; I have checked each of these reports and can conclude only that the existence of panoistic beetles has not been established. All of the beetles that have been said to be panoistic might have been expected to contain telotrophic ovarioles. Furthermore, the nutritive cords of telotrophic beetles are not usually as conspicuous as those found in Hemiptera, and may even be absent in some [Bryan (17)]. The criterion for distinguishing between panoistic and telotrophic ovarioles is the presence of trophocytes in the germarium. In the absence of nutritive cords, a detailed study of oogenesis is often required to determine whether the apical cells of the germarium are oogonia or trophocytes.

The differences between the telotrophic ovarioles of Hemiptera and Coleoptera are numerous. Schlottman & Bonhag (86) have compared the ovarioles of the milkweed bug and the adult mealworm in some detail. Although these two insects can not be said to represent respectively all of the Hemiptera and the Coleoptera-Polyphaga, they do illustrate many of the important differences between the telotrophic ovarioles of the two orders. The presence of telotrophic ovarioles in the two orders is probably an example of convergent evolution.

Polytrophic Ovary

Most of the holometabolous orders contain insects with polytrophic ovarioles but, as already noted, certain beetles have telotrophic ovarioles; the fleas are panoistic and possibly certain Neuroptera have telotrophic ovarioles. Among the Hemimetabola, the Dermaptera [Brauns (16)], Psocoptera [Goss (29)], Anoplura and Mallophaga [Ries (84)] are known to have polytrophic ovarioles.

The earwigs have simple ovarioles that illustrate all of the essential features of the polytrophic type. The earwig ovary has been studied by Brauns (16), Kornhauser (54), Bonhag (13), and Arnold (4). I have drawn freely from their writings in assembling the following account.

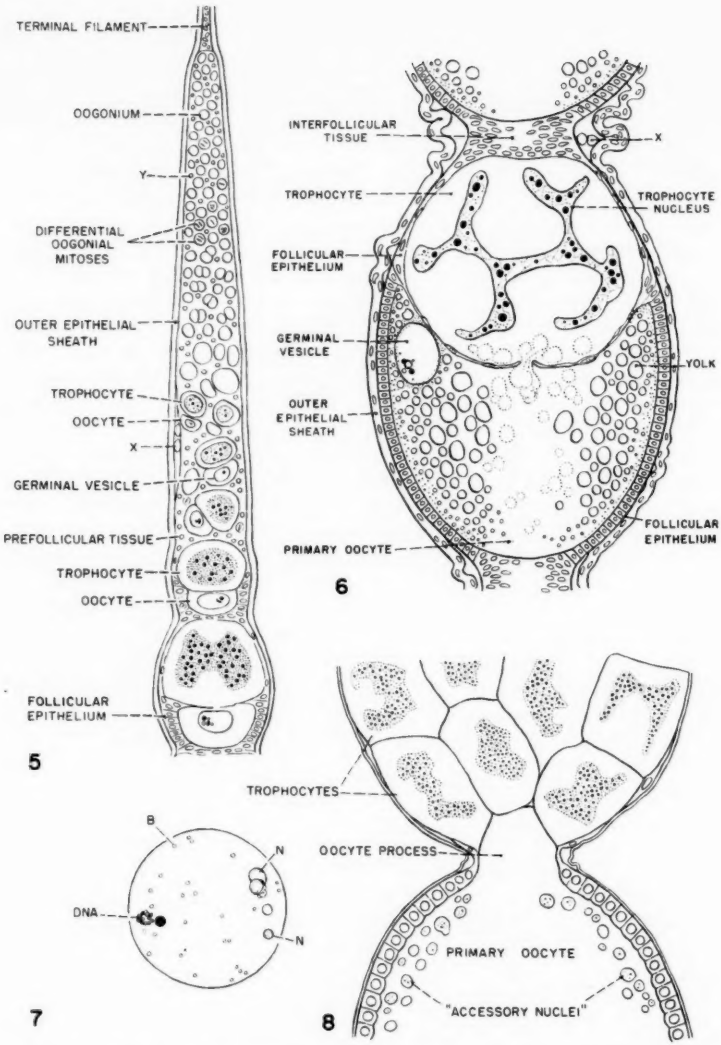


FIG. 5. Diagram of the anterior region of an ovariole of *Anisolabis maritima* [reconstructed from Kornhauser (54) and Arnold (4)]. *X*, type of cell found occasionally beneath outer epithelial sheath; *Y*, interstitial nucleus.

FIG. 6. Sagittal section of a middle-aged follicle from the ovariole of *A. maritima* [after Arnold (4)]. *X*, type of cell found occasionally beneath outer epithelial sheath.

FIG. 7. Germinal vesicle of *A. maritima*, taken from an nearly full-grown oocyte [after Arnold (4)]. *B*, particles which may be emission bodies; *DNA*, desoxyribonucleic acid-positive spherules; *N*, nucleolus-like body.

FIG. 8. Longitudinal section of a portion of the ovariole of the queen honey bee, showing a portion of a nutritive follicle and an oocyte-containing follicle.

Each ovary of the seaside earwig, *Anisolabis maritima* (Géné) is composed of five ovarioles. Figure 5 is a diagram of the anterior region of an ovariole. The usual *terminal filament* is present. Note that the germarium is not clearly marked off from the anterior end of the vitellarium. A syncytial, *outer epithelial sheath* encloses the ovariole. Irregular cells (*X*) are found beneath the outer sheath (Figs. 5, 6); it is not known whether these cells are remnants of an inner envelope, such as that found in the milkweed bug, or whether they are blood cells, as suggested by Kornhauser (54). Striated muscle fibers are associated with the outer epithelial sheath, a condition known to occur in many other insects [Imms (47)].

According to Kornhauser (54), the anterior end of the germarium is occupied by oogonia; *differential oogonial mitoses* occur about 0.1 mm. posterior to the attachment of the terminal filament (Fig. 5). The sister cells, produced by these differential divisions, are destined to have very different functions. One cell will become the *oocyte* and the other will differentiate into a nurse cell or *trophocyte*.

In the lower part of Figure 5 the pairs of *oocytes* and *trophocytes* are lining up in a single row to form the follicles of the vitellarium. The oocyte is always found posterior to its attendant trophocyte. Before the trophocyte and oocyte become oriented in line, they are surrounded by *prefollicular tissue*. Later the prefollicular tissue becomes organized into a one-layered *follicular epithelium* with distinct cell boundaries. In the course of development of the oocytes, the surrounding follicular epithelium becomes columnar, then cuboidal, and finally flattened. The follicular cells are at all times mononuclear. Mitotic divisions occur in the prefollicular tissue, and in the columnar follicular cells. Thus the follicular epithelium accommodates itself to the increasing volume of the oocyte by the following means: during the early growth phases of the oocyte, prior to active yolk deposition, mitotic division and growth of the follicular cells are most important; later, during the period of yolk deposition, the follicular cells cover the expanding surface of the oocyte by growth and change in shape.

Scattered among the germ cells, in the upper part of Figure 5, are interstitial nuclei (*Y*); these appear to be imbedded in a common cytoplasm which ramifies throughout the germarium. The interstitial nuclei are probably part of the prefollicular tissue which will later be incorporated into the epithelium of future follicles. Since the fate of the interstitial nuclei has not been completely established, it is probably best to give them a designation separate from that of the prefollicular tissue.

Figure 6 is a sagittal section of a middle-aged follicle. Both the *trophocyte* and *primary oocyte* have enlarged tremendously and the oocyte has just surpassed the trophocyte in volume. In earlier stages the trophocyte was consistently larger than its accompanying oocyte (Fig. 5). Before the yolk-filled oocyte is ovulated it will dwarf the trophocyte. Finally the trophocyte will undergo dissolution and the oocyte will be released into the pedicel.

The *trophocyte nucleus*, in Figure 6, is greatly extended and this is its

characteristic form during the period of vitellogenesis. Arnold (4) has demonstrated, through the use of the Feulgen reaction, that the DNA-positive chromatin occurs in the form of fine granules. The numerous large nucleoli in this "amoeboid" nucleus are not Feulgen-positive and are not to be regarded as condensed chromatin as reported by Brauns (16) for *Forficula*. The developmental history of the trophocyte nucleus, as outlined by Arnold, is an interesting one. In the young trophocytes, the small nuclei are spherical and contain relatively few Feulgen-positive chromatin granules (Fig. 5). As the trophocyte grows, its nucleus enlarges prodigiously and there is a concurrent increase in the number of nucleoli and Feulgen-positive granules. Later the rapidly expanding nucleus becomes "amoeboid" in shape and, as the nucleus approaches its maximum size, the Feulgen reaction becomes less intense. As we see in Figure 6, the chromatin becomes a rather inconspicuous feature of the trophocyte nucleus. It is clear from Arnold's account, that the DNA content of the trophocyte nucleus increases tremendously during its early differentiation.[6] The faintness of the Feulgen reaction in the largest trophocyte nuclei may be either the result of decreased concentration of DNA or actual reduction in the amount of DNA.

The *follicular epithelium* in Figure 6 has undergone regional specialization. Around the trophocyte, the follicular cells are squamous and sometimes rather indistinct. On the other hand, at this stage, the follicular cells surrounding the oocyte are cuboidal. A septum of squamous follicular cells has pushed in between the trophocyte and the oocyte, leaving only a median pore between the two cells. The *interfollicular tissue*, as we have already pointed out, is derived from the prefollicular tissue.

The oocyte in Figure 6 is a *primary oocyte* and its nucleus is in a modified prophase of the first maturation division. Arnold (4) has found oocyte nuclei in the germarium containing tetrads. Later the nucleus transforms into a *germinal vesicle* of the type illustrated in Figures 6 and 7. The germinal vesicle has increased greatly in volume and the individual chromosomes can no longer be identified. Instead, Feulgen-positive material can be detected in the

[6] An increase in the DNA content of the trophocyte nucleus is known to occur in a number of insects, including *D. melanogaster* [King *et al.* (51)]. In *Drosphila* the condition of the trophocyte chromosomes in relation to the DNA increase has not been established: Painter & Reindorp (74) have reported that the largest trophocyte nuclei may become 512-ploid by endomitosis; Hsu & Hansen (45) disagree; King *et al.* (51) have suggested the possibility of polyteny. Schrader & Leuchtenberger (88) have presented quantitative data which indicate that the large trophocyte nuclei of the bug, *Acanthocephala*, are formed by nuclear fusions. There are quite a number of papers on trophocyte nucleus differentiation, more than can be cited here. Two interesting papers were received after the completion of this review. One of these papers deals with endomitosis and polyteny in *Calliphora* [Bier, K., *Chromosoma*, **8**, 493–522 (1957)] and the other covers the differentiation of the trophocyte nucleus of the silkworm [Colombo, G., *Rend. accad. nazl. Lincei*, **22**, ser. 8, 64–71 (1957)].

form of a small aggregate of spherules (Fig. 7, *DNA*). The most conspicuous elements in the germinal vesicle, at this time, are the relatively large, nucleolus-like bodies (*N*). Dispersed throughout the germinal vesicle are smaller particles which have been regarded by some authors as emission bodies (*B*). We shall discuss the matter of emission bodies in a later section of this review.

Two genera of earwigs, *Hemimerus* and *Arixenia* contain viviparous species of the pseudoplacental type [Hagan (35)]. The ovary of *Hemimerus talpoides* Walker has acquired a number of interesting features. The maturation divisions of the oocyte are completed in the vitellarium and embryonic development takes place while the egg is still in its follicle. The egg lacks both chorion and yolk. According to Heymons (39) another nutritive substance occurs in the egg which is described as being fat-like. In the absence of yolk, the embryo is nourished in the follicle by anterior and posterior pseudoplacental organs. The pseudoplacental organs are formed by proliferation of the follicular epithelium, and the anterior pseudoplacental organ encloses the reduced trophocyte.

Except for the earwigs, few insects have only one trophocyte for each oocyte. According to Paulcke (76) the ratio of trophocytes to oocytes in the honey bee is 48 to 1. In many advanced polytrophic ovarioles, the wall of the ovariole has become constricted in such a way that the *primary oocyte* and its associated *trophocytes* are found in separate follicles (Fig. 8); a nipple-like *oocyte process* usually extends into the nutritive follicle.

In the diving beetle, *Dytiscus marginalis* Linnaeus, a single oogonium gives rise to 15 nurse cells and one oocyte [Giardina (28)]. Hegner & Russell (38) have found that the gyrinid, *Dinuetes nigrior* Roberts, produces seven nurse cells for each oocyte. The ultimate oogonium divides to produce a small nurse cell and a larger oocyte grandmother cell; the latter contains a peculiar chromatic body in its cytoplasm, the "oocyte determinant." The original nurse cell then undergoes two successive divisions producing four trophocytes. The oocyte grandmother cell, on the other hand, undergoes two differential divisions which produce three more trophocytes and a single oocyte. Of the eight cells ultimately produced, only the oocyte contains the determinant. The oocyte determinant persists for a while in the growing oocyte and then disappears. The reality of the oocyte determinant has been established for a few aquatic beetles but is not known to occur in other insects. Although several possible explanations have been offered, e.g. Wieman (102), Hegner (37), we do not understand the mechanism that determines why most of the daughter cells of an oogonium become trophocytes and one is destined to become an oocyte. Nevertheless, it is generally accepted that the ratio of trophocytes to oocytes in polytrophic ovarioles is fixed in each species.

Origin of Ovarian Tissues

A detailed account of the origin and development of the insect ovary is beyond the scope of this review but some mention of the present status of

the problem seems necessary to round out our consideration of ovarian histology.

The embryonic segregation of germ cells from somatic cells seems to take place at different times in the various orders and families of insects. In some insects the primordial germ cells are recognizable before the blastoderm has been completed. In certain other insects the germ cells can not be distinguished from somatic tissue-forming cells until the coelomic sacs of the embryo are formed. In all cases, however, the germ cells become fully enveloped by mesodermal tissue to form the gonad anlage. Consult Seidel (89), Nelsen (72), Hodson (40), Johannsen & Butt (48) and Krause (55) for further details on this subject.

Insect histologists of the 19th Century were much concerned with the problem of determining which cells of the adult ovary were of germ cell origin and which were of somatic (mesodermal) origin. Opinion was divided: one group maintained that the germ cell line produces only the oocytes and trophocytes; the most widely held opinion, however, was that the germ cells produce the oocytes, trophocytes, and follicular epithelium. Gross (33) has presented an interesting account of this controversy up to 1903. Although this matter has not been completely resolved, modern research supports the idea that only the oocytes and trophocytes are products of the germ line; all other ovarian tissues are probably of mesodermal origin. See, for example, the developmental studies of Wieman (102), Seidel (89), Lautenschlager (57), Nelsen (71), and Wick & Bonhag (101).

Experimental proof as to the origin of the various ovarian tissues in *Drosophila melanogaster* Meigen has been supplied by the exciting researches of Geigy (27) and Aboim (1). The posterior pole plasma of the egg is the site of segregation of the primordial germ cells of this insect. Geigy selectively irradiated with ultra-violet light this region of the egg and destroyed the primordial germ cells. The embryos developed in a normal fashion. Adult males and females were obtained that copulated but were sterile. Histological preparations of the gonads showed that they contained small ovaries and testes completely lacking in germ cells. The mesodermal constituents of the gonads, however, were quite normal. Aboim also used ultraviolet light experiments and followed in great detail the embryonic and postembryonic development of the gonads in both normal and irradiated flies. It is obvious from his work that the follicular epithelium of the normal flies is derived from mesodermal tissue. The irradiated eggs produced flies with ovaries that contained recognizable mesodermal tissues but oocytes and trophocytes did not appear because of the prior destruction of the germ line. The follicular epithelium did not differentiate in the agametic ovarioles but the tissue that differentiates into follicular epithelium in gamete-containing ovaries was present.

VITELLOGENESIS

Before discussing the cytological and histochemical aspects of vitellogenesis, it might be useful to describe a typical insect oocyte as it appears

immediately prior to ovulation. The oocyte is typically a primary oocyte at this time. Slifer & King (90) found that oocytes of *Melanoplus* about to be ovulated were in the metaphase of the first maturation division. According to Depdolla (26) this is a condition common in insects. It is not safe to generalize on this point but one can confidently say that the oocytes of most insects are in some phase of the first maturation division at the time of ovulation. Hagan (35) has reviewed a number of exceptional insects that complete their maturation divisions in the ovary; some of these viviparous forms undergo their embryonic development in the follicles of the vitellarium.

The typical oocyte is covered with a chorion which may be thin or relatively thick, smooth or sculptured. Many authors have recognized two main layers in the chorion, the exochorion and endochorion. Beament (7), on the basis of physical and chemical properties, has recognized seven layers in the chorion of *Rhodnius prolixus* Stål, five of these layers belong to the endochorion and two belong to the exochorion. The chorion is secreted by the follicular epithelium but Palm (75) has recognized two types of follicular cells in the egg follicles of bumble bees; the smaller cells appear to secrete actively during yolk formation but later degenerate and do not take part in the production of chorion. A micropylar area is present in the shell of insect oocytes to allow for fertilization. Several viviparous species of insects do not produce an egg shell [Hagan (35)]. Beneath the chorion is the vitelline membrane.

By the time the primary oocyte is ready to be ovulated, yolk deposition has been completed. The main deutoplasmic substances in the oocyte are the protein yolk bodies, the lipide yolk bodies (coarse sudanophilic bodies), and glycogen particles. The protein yolk bodies are extremely numerous and usually account for most of the volume of the oocyte. The lipide yolk bodies are distributed among the protein bodies. There is histochemical evidence that glycogen may not be present in the oocytes of all insects [Bonhag (11)]. When present, glycogen particles can be found in the spaces between the protein yolk bodies [Ries (84), Bonhag (13), etc.]. The eggs of some viviparous insects contain little or no yolk of the usual type [Hagan (35)].

The cytoplasm of the fully grown oocyte is not often very conspicuous. Some of the cytoplasm is usually concentrated at the periphery of the oocyte and is known as the periplasm, "Keimhautblastem," or cortical cytoplasm. At the time of ovulation, the germinal vesicle is usually located to one side of the oocyte and the periplasm may be more extensive in this area. Sometimes the periplasm projects rather deeply into the yolk field at the anterior pole of the oocyte [Tiegs & Murray (96)]. In some insects, specialized cytoplasm at the posterior pole of the egg is distinguishable; this pole plasm constitutes the germ tract determinant which plays a role in the embryonic segregation of the germ cells [Hegner (36)]. A cytoplasmic reticulum typically extends from the periplasm and ramifies through the yolk-laden interior of the oocyte. Symbiotes have been found in the oocytes of a number of different insects [Wigglesworth (103)].

Cytological Studies

Practically every cellular structure known to the light microscopist has, at one time or another, been reported to produce (or transform into) insect yolk. Many of the conclusions found in the extensive literature are not very solidly supported. It appears that the exclusive use of classical staining techniqnes in the investigation of insect yolk formation has reached the point of diminishing returns. Nevertheless much important information has resulted from these studies. The following conclusions deserve careful consideration in connection with future research.

Origin of protein yolk.—During the period of oocyte growth and yolk deposition, the germinal vesicle attains its greatest dimensions and undergoes remarkable internal changes. The germinal vesicle of the grasshopper, *Melanoplus differentialis* (Thomas), may attain a diameter of 150 μ and has been observed to oscillate rhythmically during the period of yolk deposition [Tahmisian *et al.* (95)]. In many insects, nucleolar emissions have been reported to migrate through the fluid of the germinal vesicle and to pass into the oocyte cytoplasm. I have described earlier in this paper two types of germinal vesicles (Figs. 2 and 7) and the reader is referred to Bauer (6) for a more extensive comparative picture of the germinal vesicle.

Before passing on to the significance of the so called "emission bodies," we should take note of a recent reinterpretation of the germinal vesicle. Mulnard (67) has studied the germinal vesicle of the weevil, *Acanthoscelides obtectus* (Say), both *in vivo* and in sectioned tissue. The fluid-filled germinal vesicle contains a large, nucleolus-like "caryonucléole" which gives a faint Feulgen reaction. During vitellogenesis emission bodies are released from the caryonucléole. Mulnard concluded that the caryonucléole represents the true nucleus of the oocyte and has demonstrated that, in the course of maturation, the chromosomes reappear there. Mulnard did not believe that the oocyte nucleus simply grows to become the germinal vesicle: rather he maintained that the caryonucléole is the oocyte nucleus; the fluid, which accounts for the bulk of the volume of the germinal vesicle, he regarded as being a new substance, enveloping the true nucleus.

Nucleolar extrusions from the germinal vesicle of the American roach and Oriental roach have been reported to give rise to the protein yolk bodies [Hogben (41); Nath & Mohan (69); Gresson (32)]. The nucleolus develops internal vacuolar bodies which are said to pass out of the germinal vesicle and the bodies come to lie at the periphery of the oocyte, beneath the follicular epithelium. The emission bodies increase in size and become uniformly distributed in the cytoplasm. Finally they fragment into small particles, which enlarge enormously, eventually to form the definitive protein yolk bodies. Ranade (83) has also studied oogenesis in the roach but disagreed with the afore-mentioned authors; he found no evidence of nucleolar emissions and attributed the origin of protein yolk to oocyte mitochondria. The protein yolk bodies of the dragonfly have also been related to nucleolar emissions [Hogben (42)]. In the firefly, *Luciola*, nucleolar buds pass into the cyto-

plasm of the oocyte and, according to Nath & Mehta (68), give rise directly to protein yolk bodies. A similar process has been reported by Bhandari & Nath (9) for the bug, *Dysdercus cingulatus* (Fabricius). In the latter insect nucleolar extrusions migrate to the periphery of the oocyte and the nucleus follows suit; protein yolk bodies arise for the first time among the peripheral nucleolar extrusions. Ries (84) has found, in Anoplura and Mallophaga, that basophilic granules, the "chromidia," are relased exclusively from the germinal vesicle into the oocyte cytoplasm. The chromidia are Feulgen-negative and develop into protein yolk bodies, assisted by contributions from both the follicular epithelium and the trophocytes.

Hsu (44), in his recent study of *Drosophila melanogaster*, concluded that the protein yolk originates from nucleolar emissions. The details of this process in *Drosophila* differ from the cases of nucleolar emissions cited above in three main ways: the emissions are contributed exclusively by the trophocyte nucleolus; the emissions are "lipoidal" in nature; and the yolk precursors are said to be embedded in the nucleolar emissions. Once transported into the oocyte, the precursor bodies develop into individual protein yolk bodies.

The oocytes of some insects are known to contain vesicle-enclosed granules which superficially resemble nuclei (Fig. 8). These are the so-called "*accessory nuclei*" (secondary nuclei); they have been reported from certain Hemiptera, Lepidoptera, Coleoptera, Diptera and especially Hymenoptera [Buchner (18), Mukerji (66), Rabes (82)]. Although some of the earlier workers thought that they were true nuclei or chromatin fragments, they are no longer considered as such and are known to be Feulgen-negative [Mukerji (66)]. The "accessory nuclei" disappear before the oocyte is ovulated and a few authors have regarded them as precursors of the yolk bodies. Peacock & Gresson (78) have stated that, in certain tenthredinids, "accessory nuclei" arise from particles extruded by trophocyte nuclei, from nucleolar buds of the germinal vesicle, and possibly from the emission of granules from dark-staining cells of the follicular epithelium. This conclusion has been cited by several authors who failed to point out that it was later refuted by Gresson (31). In another paper on tenthredinid oogenesis Gresson (30) concluded that nucleolar emissions from the germinal vesicle play a part in the production of protein yolk. He did not relate the "accessory nuclei" to the problem of protein yolk production. Palm (75) has studied several species of bumble bees; in his opinion the "accessory nuclei" are not derived from nuclear or nucleolar extrusions. Instead the "accessory nuclei" are developed from secretion particles produced by the cytoplasm of the trophocytes and represent an intermediate stage of protein yolk production. The same author has produced evidence which suggests that the follicular epithelium contributes secretion granules which also grow into yolk bodies.

Steopoe (93) represents a minority opinion; he claimed that the Golgi elements of the oocyte are responsible for the production of protein yolk bodies in *Nepa cinerea* Linnaeus. On this point he disagrees with Köhler (53) and Spaul (91) who proposed a nucleolar origin for the yolk bodies in the same

species of bug. Steopoe reported that Golgi elements pass from the trophocytes, by way of the nutritive cords, to the oocytes. These Golgi elements together with the indigenous Golgi elements of the oocyte are said to develop into the protein yolk.

Several authors have suggested that the protein yolk bodies are of mitochondrial origin. We have already noted that Ranade (83) came to this conclusion in his study of the American roach. Hegner (36) found that mitochondria (bodies stained with crystal violet after Benda's method) multiply as the oocyte of *Leptinotarsa decemlineata* (Say) grows. The mitochondria increases rapidly in size and number and are concentrated at the periphery of the oocyte. The mitochondria gradually lose their affinity for crystal violet as they enlarge to form the large yolk bodies. Machida (59) has stated that the protein yolk of the silkworm originates from the follicular cells, the mitochondria of which transform into yolk or, at least, take some part in its formation.

Origin of lipide yolk.—Many authors have concluded that the Golgi elements of the oocyte develop into the lipide yolk bodies. A few examples will serve our purposes. According to Nath & Mohan (69) the Golgi elements of the American roach form a circumnuclear ring in the youngest oocytes. When the oocyte grows the circumnuclear concentration spreads out in the cytoplasm and each Golgi vesicle increases in size. As the Golgi vesicles grow and increase in number, they migrate to the periphery of the oocyte and come to lie below the follicular epithelium. The enlarged vesicles then disperse throughout the oocyte cytoplasm, become filled with fat and constitute the lipide yolk bodies. The accounts of the same process in the roach by Gresson (32) and Ranade (83) are essentially in agreement with that of Nath & Mohan. In a firefly, of the genus *Luciola*, Golgi vacuoles are said to swell up in the oocyte and give rise to lipide yolk [Nath & Mehta (68)].

Bhandari & Nath (9) claim that intact Golgi elements pass from the apical trophocytes of *D. cingulatus* by way of the nutritive cords into the oocytes. These Golgi elements presumably join the Golgi elements of the oocyte in forming the lipide yolk inclusions. According to Gresson (30), Golgi vacuoles are present in the undifferentiated germarial cells of tenthredinids; the Golgi vacuoles increase in number and size in both trophocytes and oocytes. Later the Golgi elements of the trophocytes are contributed to the associated oocyte. The Golgi material of the oocyte then develops into lipide yolk by the deposition of fat in the Golgi vacuoles.

Ries (84) in his study of chewing and sucking lice found that fatty droplets appear in the oocyte at the time that chromidia production ceases. Furthermore, Ries & van Weel (85) have stated that "lipochondria" enlarge and multiply during oocyte growth, gradually accumulate fatty material, and transform into the lipide yolk of *Pediculus*. These authors considered the lipochondria to be comparable to the Golgi vesicles of Nath and his co-workers but did not think that they could be homologized with the typical Golgi apparatus of vertebrate cells. They did not believe that lipochondria were contributed to the oocyte by the trophocytes and follicular cells.

Machida (59) has recognized two kinds of fatty yolk in the silkworm egg; one type of yolk originates from the Golgi elements of the oocyte, trophocytes, and follicle cells. The second type of lipide yolk was said to arise from nucleolar extrusions of the trophocytes.

In *Drosophila melanogaster*, according to Hsu (43), the oocyte depends upon the trophocytes for the production of fatty yolk. During the development of the trophocytes, the mitochondria proliferate; finally the chondrioconts break up into granules which enlarge and eventually all transform into lipide yolk.

Evaluation and suggestions.—By first appearances, the evidence seems overwhelming in favor of the idea that protein yolk bodies arise from nucleolar emissions; actually very few of the proponents of this idea have actually observed the passage of nucleolar buds into the surrounding cytoplasm. In most cases the conclusion was based upon the presence of particles in the cytoplasm which were comparable in size, staining capacity, or general appearance to particles in the nucleus of the oocyte or trophocyte. Although a considerable amount of circumstantial evidence favors the nucleolar emission theory, I do not believe that all other alternatives should be summarily dismissed. Additional cytological studies correlating classical staining procedures with histochemical methods would probably shed further light on the problem. The use of the electron microscope is also very promising in this respect. Perhaps knowledge of the ultra-structure of the yolk precursors in the cytoplasm and the nucleolar particles in the nuclear sap would establish or disprove the nucleolar emission theory. In many cases nucleolar emission particles of considerable size are said to pass through the unbroken nuclear membrane; electron microscopy could demonstrate whether this is possible and, if so, clarify the mechanics of particle passage from the nucleus into the cytoplasm.[7] If nucleolar emissions give rise to yolk bodies, one should be able to follow the structural transformation of the former into the latter with the electron microscope.

In the light of our present knowledge of the biochemistry and ultrastructure of mitochondria, it does not seem likely that these cytoplasmic organelles transform directly into protein or lipide yolk bodies. Nevertheless, these claims deserve reinvestigation. The electron microscopist is not dependent upon relatively non-specific staining procedures for identifying cytoplasmic organelles. For example, mitochondria can be recognized quite reliably on the basis of their ultra-structure. The electron microscope should be able to disclose whether certain cytoplasmic organelles transform into yolk or whether Payne (77) is correct in his view that lipide and protein yolk bodies

[7] Several investigators have already revealed porous nuclear membranes by the use of the electron microscope. Anderson & Beam [*J. Biophys. Biochem. Cytol.*, **2**, suppl., 439–44 (1956)] have shown that material, possibly nucleolar in origin, passes through the pores of the trophocyte nuclear membrane of *R. prolixus* into the adjoining cytoplasm. Whether this material plays a role in yolk production is yet to be demonstrated.

arise independently in the oocyte cytoplasm with the cytoplasmic organelles playing no direct, visible role in their formation.

The majority of investigators have concluded that lipide yolk originates from vesicles which may be Golgi material. The problem here seems to be the exact identification of the precursors of the lipide yolk. This problem is complicated by the controversial history of the Golgi appartus. On several occasions, the Golgi apparatus has even been declared nonexistent. Recently electron microscopists have extablished that a definite structural entity exists in the Golgi zone of vertebrates [see Novikoff (73) and Dalton & Felix (21) for references]. The question of whether the so-called Golgi apparatus of invertebrates is, in all cases, homologous to that found in the vertebrates has not yet been answered. Novikoff (73) believes this issue can be quickly settled by the electron microscopist. The study of insect vitellogenesis by electron microscopy may provide definitive answers to several problems which are of basic importance to the whole field of cellular physiology.

Histochemical Studies

Histochemical slides usually give a static impression of chemical processes. However, there are insects whose ovarioles provide an excellent linear sequence of follicles. This makes it possible to get a dynamic picture of vitellogenesis in which there is little difficulty in associating the successive chemical stages. Although much more work is needed, the histochemical papers already published have extended, corrected, and clarified some of the conclusions obtained by classical cytological studies.

The most widely used histochemical test for desoxyribonucleic acid (DNA) is the Feulgen reaction; Brachet's method (15) is widely used for the detection of ribonucleic acid (RNA). See Pearse (79) and Lillie (58) for methods and discussion. Quantitative methods for nucleic acids include the Caspersson microspectrophotometric method and the spectrophotometric method for Feulgen-treated slides. See reviews by Pollister (81) and Alfert (3). These methods have been used effectively in studies of insect oogenesis and vitellogenesis. For example, Bauer (6), Schlottman & Bonhag (86), and many others have used the tests for identifying nuclear components; Swift & Kleinfeld's (94) quantitative study of the DNA content of the developing female germ cells supports the concept that DNA is under quantitative control during grasshopper development. Measurements on meiotic phases in grasshopper oocytes have shown that DNA follows the same basic pattern described for mouse gametogenesis. Mukerji (66) has established the nonchromosomal nature of the "accessory nuclei." Urbani (98) has demonstrated that the "oocyte determinant" (Giardina's body) of *Dytiscus marginalis* contains both DNA and RNA and has found that the ooplasm of the oocyte, especially around this chromatic body, is enriched with RNA during dissolution of Giardina's body. Morgenthaler (65), Bier (10), Mulnard (67) and Colombo (20) have studied RNA localizations and concentration gradients in developing oocytes.

The possibility of nucleic acids being contributed by the trophocytes to the oocytes of insects was postulated before reliable histochemical methods were in wide use [Paulcke (76); Wieman (102); Bhandari & Nath (9)]. Using histochemical methods, Schrader & Leuchtenberger (88) have found DNA droplets in the cytoplasm of the apical trophic tissue of certain coreid bugs; these droplets were derived from the trophocyte nuclei. Although DNA droplets were rarely found in the central cytoplasmic core of the nurse tissue, it was assumed that DNA is passed on to the oocytes in the form of a Feulgen-negative, depolymerized substance. Bonhag (11) has studied a similar phenomenon in the ovarioles of the large milkweed bug; in this telotrophic insect, trophocyte nuclei pass into the central cytoplasmic core of the apical nurse tissue and migrate to the posterior end of the core. These transitory nuclei become pycnotic, and free DNA droplets accumulate near the anterior ends of the cords that lead to the oocytes. The accumulated droplets disappear and are later replaced by similarly derived DNA droplets. Since massive quantities of DNA were observed to accumulate in a cyclical fashion at the end of a one-way system leading to the oocytes, it was suggested that the DNA transforms into a Feulgen-negative substance that passes to the growing oocytes. Kaufmann *et al.* (50) have reported that the trophocytes of *Habrobracon* become polyploid as the result of endomitosis; eventually the nurse cells disintegrate and DNA from the trophocyte is said to pass into the oocyte cytoplasm. This DNA is quickly broken down and dispersed throughout the egg, perhaps to serve as reserve DNA building blocks.

Morgenthaler (65) and Bier (10) have presented circumstantial evidence to the effect that RNA is contributed by the trophocytes to the oocytes in the honey bee. In the large milkweed bug, RNA also appears to be contributed by the trophocytes to the oocytes. Bonhag (11) has found a continuous, flow-like pattern of RNA extending from the cytoplasm around the trophocyte nuclei, into the trophic core, and through the nutritive cords into the oocytes.[8] According to Dasgupta & Ray (22) the RNA-rich, trophocyte nucleolus of the bedbug extrudes DNA. The latter is said to move to the nuclear membrane and pass "into the cytoplasm again as RNA and perhaps as a low polymer of DNA." These substances were said to pass down the nutritive cords into the oocyte. The observations presented by these authors hardly prove these conclusions; their evidence for the RNA-DNA turnover at the periphery of the nucleolus is particularly inadequate. Dasgupta & Ray (23) have made similar claims for the follicular epithelium; here again, their histochemical evidence is subject to alternative explanations.

Little is known about the chemical nature of the protein yolk bodies of insects except that they are protein-positive and are known to be periodic acid-schiff (PAS) reactive in a number of cases [Colombo (20); Bonhag (11,

[8] I received, after the completion of this review, a paper on silkworm oogenesis which demonstrates that the trophocytes of this polytrophic ovariole discharge RNA into the oocyte [Colombo, G., *Boll. Zool.*, **23**, 279–89 (1956)].

13)]. The PAS-reactivity of the protein yolk bodies probably results from the presence of a carbohydrate-protein complex, possibly muco- or glyco-protein [Bonhag (11, 13)]. In the large milkweed bug and the earwig, the PAS-reactivity of the protein yolk bodies is certainly not due to the incorporation of glycogen. It is interesting to note that, in an early (1923) biochemical study of the silkworm egg [cited by Needham (70)], Pigorini found that 50.9 per cent of the total protein yielded glucosamine upon hydrolysis, indicating the presence of an ovomucoid.

Bonhag (12) has applied histochemical tests for lipides to frozen sections of the large milkweed bug and has found that sudanophilic lipides are contributed to the oocyte by both the follicular epithelium and the trophocytes. The lipide yolk bodies are first formed in the oocyte from precursor bodies which apparently utilize lipides obtained from the apical trophic tissue. Later most of the lipide yolk bodies are formed from precursor bodies lying near the follicular epithelium. The precursor bodies of the lipide yolk of the milkweed bug probably correspond to the "Golgi vesicles" of Nath and the "lipochondria" of Ries and van Weel (see previous section of this review). In the milkweed bug there is a progressive increase in amount of phospholipides in the oocyte until the later stages of yolk production; from this point on there is a reduction in the amount and distribution of acid haematin-stained phospholipides until, in the last follicle, phospholipides are restricted to a narrow area at the periphery of the oocyte.

Glycogen is dispersed throughout the eggs of Anoplura; it appears in the oocyte at the time that the yolk is about complete [Ries (84)]. In the honey bee, according to Bier (10), glycogen particles suddenly appear in the large posterior oocytes of the vitellarium. By the time the glycogen is deposited the trophocytes have already disappeared; Bier believes that the follicular cells contribute the glycogen. Palm (75) came to the same conclusion in regard to the bumble bee. In *Anisolabis maritima*, glycogen appears first in the trophocyte. The glycogen accumulates and is discharged directly through the median pore of the trophocyte into the oocyte [Bonhag (13)]. Here again, glycogen is added to the oocyte during the late phases of vitellogenesis. Although glycogen may be present in the oocytes of most insects, it is apparently lacking in the large milkweed bug [Bonhag (11)].

Two main periods of oocyte growth generally can be recognized in insects: the first period occurs prior to yolk deposition and the second is the period of greatest enlargement during which large quantities of yolk are deposited.[9] King, Rubison & Smith (51) have calculated that the volume of the ooplasm of *D. melanogaster* increases in three days by 100,000 times because of the deposition of yolk.

There is general agreement that the trophocytes contribute to the great enlargement of the oocyte in meroistic ovarioles. Many workers have ob-

[9] See Colombo (19, 20) for a refinement of this concept in which he distinguishes three periods of oocyte growth.

served stainable particles streaming from the trophocytes to the oocytes and histochemical studies have served to clarify this relationship. For example, I have shown that proteins, lipides, RNA, and DNA derivatives are in all probability contributed by the trophocytes to the oocyte in the large milkweed bug [Bonhag (11, 12)]; direct evidence has been obtained which shows that glycogen, as well as other PAS-positive substances, are contributed by the trophocyte of *Anisolabis* [Bonhag (13)]. On the other hand, the nutritive role of the follicular epithelium is not as well established: a number of authors have maintained that, in the particular insects they studied, the sole function of the follicular epithelium is to secrete the chorion [Köhler (53); Wieman (102); Hsu (43), etc.]. Brauns (16) has gone so far as to say that in all meroistic ovarioles the task of supplying the oocytes with nutrients falls exclusively to the trophocytes. Recent histological and histochemical studies have disproved the universality of this generalization [Palm (75); Bier (10); Bonhag (12)]. Not only are lipides and carbohydrates contributed to the oocytes of some insects by the follicular epithelium; the follicular epithelium also plays an important role in the development of protein yolk bodies [Bonhag (13)].

In concluding this discussion, I would like to emphasize several points. We have evidence that histochemistry is a productive approach to the problem of vitellogenesis because it makes possible intracellular chemical localizations but much more work is needed along this line. Obviously the deutoplasm of the egg is the main nutritional substrate upon which the embryo must draw during its development. Therefore information on the origin, distribution, and nature of yolk is of fundamental importance to studies of embryonic nutrition. Histochemical studies can provide significant leads for future research but ultimately adequate understanding of the chemical composition of insect yolk will have to rely on biochemical analysis. Fortunately these analyses can be facilitated by the availability of methods, such as differential centrifugation, for physical separation of the various yolk particles. Separation of the main chemical constituents of the various deutoplasmic bodies can be expedited by electrophoretic and chromatographic procedures.

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GENETICS AND BREEDING OF THE HONEY BEE[1,2,3]

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The honey bee, *Apis mellifera* Linnaeus, like Indian corn and the domestic silkworm, is both an economically valuable species and a favorable one for genetic research. Apiculture at present is one of the world's significant minor industries. Even though man, in most regions of the world, is not as dependent on honey bees for wax and concentrated sugars as he once was, it is likely that he is becoming more dependent upon them for pollination of fruits, vegetables, and seed crops. This dependence springs from several agricultural practices that destroy wild pollinating insects.

Honey bees have contributed to the advancement of science in impressive ways. Published researches of Swammerdam, von Siebold, Boveri, D. Keilin, G. F. White, Snodgrass, and von Frisch have dealt with bees in one way or another. The discovery of parthenogenesis in bees by Dzierzon was an important advance in knowledge of reproduction. Moreover, it may have been Dzierzon's counts of black and yellow drones from the unfertilized eggs of a hybrid queen that suggested to Mendel the new idea of classifying and counting progeny of each mating [Zirkle (126, 127)]. Such a technique, applied by Mendel to more complicated diploid species, enabled him to make the first profound break in the study of heredity.

Although Mendel and other early investigators experimented with bees, the study of bee genetics was hampered until the technical genius of Lloyd R. Watson was brought to bear upon the problem of mating control. Watson devised artificial (instrumental) insemination for this insect in 1926 (11, 119, 120). The Watson technique soon was utilized by other workers, and eventually, greatly improved. Nolan (68), Laidlaw (40, 41), Mackensen (50, 51, 53, 55), and Mackensen & Roberts (58), principally, deserve great credit for improving the technique and making the apparatus and instruments commercially available (Fig. 1 and 2). Apparently the honey bee is still the only insect that can be inseminated instrumentally with high success.

This paper will deal primarily with material published since the excellent

[1] The survey of the literature pertaining to this review was completed in June, 1957.

[2] Journal Paper No. J3233 of the Iowa Agricultural Experiment Station, Ames, Iowa. Project No. 1332. Preparation of this paper was supported in part by a research grant E599(C6) from the National Institute of Allergy and Infectious Diseases of the National Institutes of Health, Public Health Service.

[3] I should like to dedicate this review to the memory of Dr. O. W. Park, whose work gave an impetus to bee breeding and genetics. My appreciation, for their assistance, is expressed to Dr. John W. Gowen, Dr. Willard F. Hollander, and Mr. Victor C. Thompson.

reviews of Ruttner & Mackensen (103) and Kerr & Laidlaw (39), and with material on breeding not covered by them.

Cytology, Development, and Sex Determination

Genetics and breeding of honey bees develop more surely if based on a knowledge of this insect's morphology, physiology, and cytology. It is a matter of good fortune for students of honey bees that Snodgrass has written on anatomy of the honey bee repeatedly, and most recently in 1956 (108). Honey-bee embryology was studied extensively by Nelson in 1915 (66). Johannsen & Butt reviewed the subject briefly in 1941 (35). Snodgrass (108) cites several papers on postembryonic development to which should be added the study by Myser (65).

There are no compilations covering the whole of honey-bee physiology that equal those in anatomy. Nevertheless, much original literature exists in this field and honey-bee physiology is discussed frequently by Wigglesworth (123) and by the various authors in Roeder's book (92). Significant new work in honey-bee physiology is appearing frequently.

Cytological origin and development of normal individuals.—Except for recent brief reviews, cytological information is even more scattered. Much of the work in honey-bee cytology was done many years ago, but recent work by Manning (60, 61, and other papers) has created new interest. Prior to Manning the concensus was that the female gonial cells possess 32 chromosomes and the male gonial cells 16. Manning presented some evidence for the elimination of one chromosome in spermatogenesis leaving sperms with only 15 chromosomes. Females, developing from the zygote composed of one gamete from the mother and one from the father, would have 31 chromosomes. The weight of evidence as discussed by Sanderson & Hall (106), Ruttner & Mackensen (103), and Kerr & Laidlaw (39) strongly indicates that there are 16 chromosomes in gonial cells of males, and 32 in those of females. Hachinohe & Onishi (32) found 16 chromosomes in all stages of meiosis in the drone. Consequently, it seems that gametes produced by both drones and queens carry 16 chromosomes.

Terminology designating drones as haploid and females as diploid sometimes becomes tangled. Degrees of ploidy in the somatic tissue and the evolutionary origin of the set of 16 chromosomes are the trouble makers. The evolutionary origin of the 16 chromosomes should be treated as a separate problem. Transmission of mutations in bees is straightforward and no polyploid ratios have been observed. So, regardless of the origin of the 16 chromosomes, the drone is a haploid and the female a diploid in reproductive and genetic processes.

Even though gonial cells possess 16 or 32 chromosomes, Sanderson & Hall state that cells of certain differentiated somatic tissues of both male and female may have twice or four times as many chromosomes as expected—32 or 64 in males, 64 or 128 in females. Such a state of affairs is not at all unexpected, for as White (121, pp. 33 to 34) states,

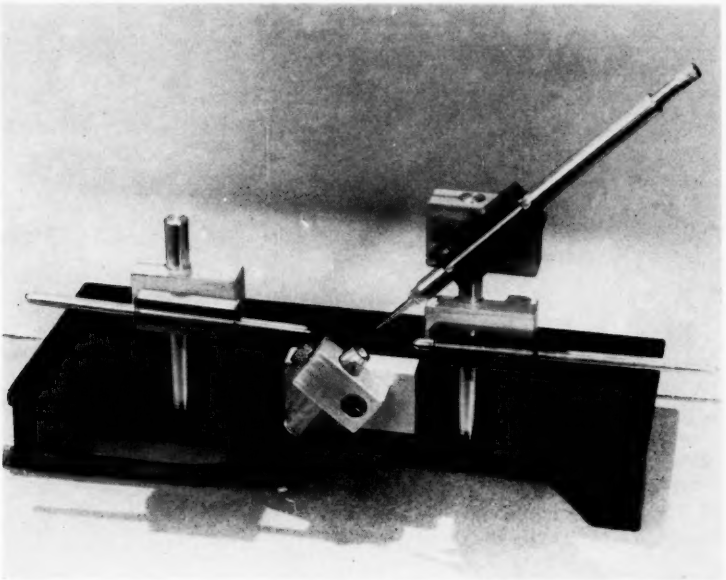

FIG. 1. Mackensen queen-bee insemination apparatus showing plastic tube in which the queen is held, hooks at each side used to hold the abdominal plates of queen open, and the syringe with which semen is taken up and injected into the queen. Carbon dioxide anesthetic flows through the rubber tube and queen holder. A binocular stereoscopic microscope also is used. (Photograph courtesy of Dr. Otto Mackensen)

The whole process of histological differentiation in insects seems to be intimately bound up with this phenomenon of endopolyploidy, each organ and tissue having its own characteristic degree of ploidy, some being entirely composed of one type of cell, while others are mosaics of cells with different multiples of the fundamental diploid number.

Along this line, two papers have appeared recently and almost simultaneously on the problem. Merriam & Ris (62) studied nuclear size and desoxyribosenucleic acid content of nuclei in several honey-bee tissues, but principally in Malpighian tubules and intestine of queen, drone, and worker. Desoxyribosenucleic acid content is a reflection of the chromosome content of the nucleus. High degrees of polyploidy were found in somatic tissues. Particularly interesting is the question of differences in numbers of chromosomes in male and female somatic tissues. The authors concluded, "Male tissues have about the same chromosome numbers as comparable female tissues."

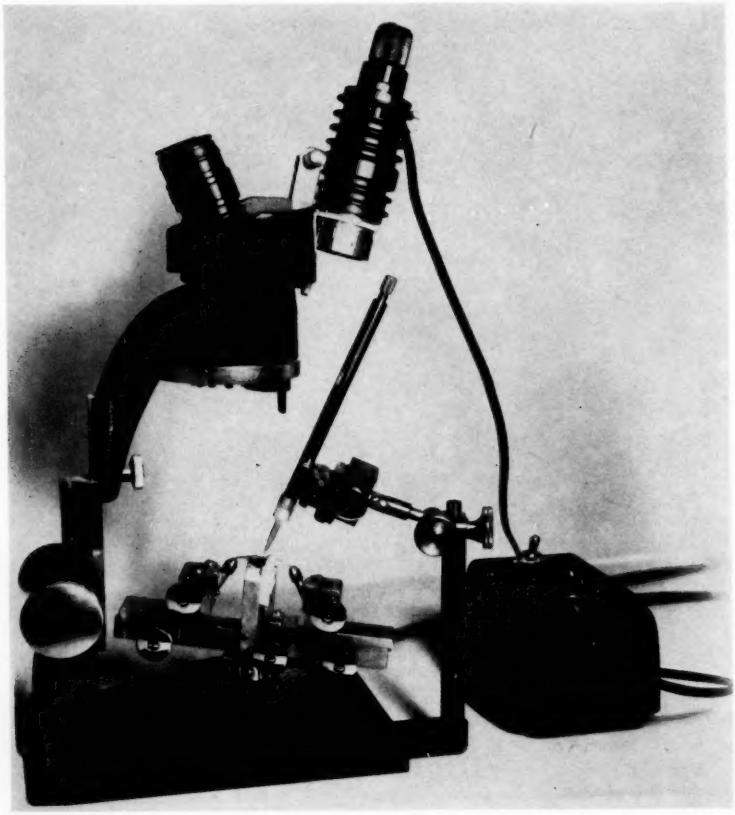

FIG. 2. Laidlaw queen-bee insemination apparatus showing queen held in place. Hooks and syringe are moved by rack and pinion adjustment. Carbon dioxide anesthetic used. (Photograph courtesy of Dr. Harry H. Laidlaw)

Risler (89), in an extensive investigation, studied somatic polyploidy throughout the course of development in drones and workers. Tissues investigated were epidermis, trachea, various regions of the intestine, brain, muscle, dorsal diaphragm, fat body, gonads, and blood cells. High degrees of polyploidy were found. It was found that the tissues become polyploid at different stages in development and the time, place, frequency, and manner of increase in chromosome number are essential features of development.

In spite of nutritional differences, it has seemed paradoxical that drones are so similar in body size to queens and actually larger than workers. Size

of eye facets and number of microcheatae per unit area of wing surface suggest that male cells are larger than female cells. If this is true, it may find its explanation in endopolyploidy. Further work along the lines of that reported by Merriam & Ris and by Risler would seem to be of great significance for increased understanding of developmental physiology in queens, drones, and workers.

Cytological origin of exceptional individuals.—Exceptional individuals include (*a*) mosaic males, (*b*) mosaic females, (*c*) gynandromorphs, (*d*) impaternate females, and (*e*) mosaic individuals having biparental male tissue. Most of these types have occurred in appreciable numbers. In most cases, these numbers have been too limited, nevertheless, for analysis by cytological methods. Instead, cytological processes have been inferred from genetical results involving transmission of marker genes.

(*a*). Tucker (117) reported three mosaic males produced by heterozygous unmated queens. These appeared to be normal drones in every respect other than the mosaicism. Tucker proposed that they arose from two of the nuclear products of meiosis.

(*b*). Taber (114) reported fourteen females that were mosaic for two genetically different kinds of tissue. To account for the mosaicism, he advanced the explanation of binucleate eggs fertilized by two sperms.

(*c*). Gynandromorphs may arise in various ways. Mackensen (52) discussed one individual in which female parts were biparental and male parts maternal in origin, which recalls the Boveri hypothesis of partial fertilization. Tucker (117) found five gynandromorphs produced by unmated queens. Since both the male and female tissues of these gynandromorphs were maternal in origin, they will be discussed along with impaternate females. Rothenbuhler, Gowen & Park [(94) and earlier papers] developed a line of bees that produced gynandromorphs in high frequency. Thousands of gynandromorphs have been observed, and all but a small number of exceptional specimens have been produced by zygogenesis and androgenesis. Female parts develop from the zygote formed by fertilization of the egg pronucleus by a sperm, and consequently, are of biparental origin. Male parts develop from one or more accessory sperms in the cytoplasm of the egg, and thus, are of paternal chromosomal origin. This gynandromorph-producing line can be used to attack a great many morphological and physiological problems in honey bees (94). Sakagami & Takahashi (104) have studied behavior in about 40 dynandromorphic bees.

(*d*). Production of female progeny by parthenogenesis was not known to occur in other than some African varieties of honey bees prior to 1943. At that time, Mackensen (49) published clear evidence that females were produced from unfertilized eggs in three strains with which he worked. Tucker recently completed an extensive study on the origin of such impaternate females. By any standards, such individuals are not plentiful, but Tucker learned in the course of his work that a higher percentage of them was produced from eggs laid when the queen's oviposition rate was increasing after a

period of restricted, or no, oviposition. Furthermore, all lines in every race tested produced them.

Tucker's experiments utilized unmated queens that were heterozygous at one or more genetic loci. By an analysis of segregation of mutant genes in workers from unfertilized eggs, and of the frequency of their occurrence in relation to oviposition rate of the queen, he was enabled to present an explanation involving misorientation of the spindle of the first meiotic division. Instead of projecting into the egg, the misoriented spindle lay parallel to the egg surface. The second meiotic division of the two products of the first division then produced two pronuclei and two polar bodies instead of one pronucleus and three polar bodies. The two pronuclei then underwent syngamy, formed a zygote, and gave rise to a female. Tucker concluded that longer-than-normal retention of the egg produced some change leading to spindle misorientation. Upon initiation of oviposition, these eggs were laid and some impaternate females resulted.

Tucker's gynandromorphs from unmated queens were explained similarly. He suggested that the two egg pronuclei underwent cleavage and then one product of each underwent union to form female tissue. The male tissue would arise from the remaining haploid nuclei.

(*e*). Male tissue of biparental origin has been found for the first time [Rothenbuhler (94, 95)]. Several investigators [most notably Mackensen (52)] have looked for diploid males among the progenies of appropriate matings. None have been found, presumably, because of the high inviability of such individuals. It seems, however, that diploid male tissue can survive in mosaic combination with viable haploid male tissue. At any rate, diploid male tissue (instead of female tissue) was found in mosaic combination with haploid male tissue in some individuals among "normal" gynandromorphic progeny. Mackensen's data (52, 54) on inviability of progeny produced by matings of closely related individuals, taken with the discovery of diploid male tissue (95), constitute strong evidence for the multiple sex-allele hypothesis of sex determination in honey bees.

The multiple sex-allele hypothesis was developed from results in *Habrobracon*. Whiting (122) reported nine different alleles at a single genetic locus or chromosome segment. Any heterozygous combination of alleles led to female differentiation. Any homozygous combination of alleles led to male differentiation if the individual was viable. Any haploid was hemizygous at the sex locus and developed into a normal male.

Mutations and Other Genetic Considerations

Genetic investigations gain momentum as good marker genes become available. In fact, genetic markers often provide the tools for a sound biological experiment having little or nothing to do with genetics per se. Both dominant and recessive markers are desirable, and for greatest value, they should have negligible deleterious effects on viability or behavior of the in-

dividual possessing them. Only a small start has been made in honey bees toward discovering mutations, learning their heredity, and maintaining stocks of those suitable for use as markers. Table I lists honey-bee mutations, somewhat in the manner of Bridges & Brehme (7) for *Drosophila*, and cites pertinent literature.

There is need already for clarification of certain situations in naming mutants in honey bees. For instance, it is not known whether chartreuse-1 and chartreuse-2 are at the same locus as chartreuse. It is not known whether the ivory listed second is the same as the one listed first. Rothenbuhler *et al.* (98, 99) unfortunately used a lower case *s* as the symbol for snow after Dreher had used a capital *S* for Schwarzsuchtig. It is expected that such uncertainties will be clarified soon. Workers in bee genetics are in a fortunate position. They can capitalize on the vast experience of *Drosophila* geneticists, presented in Bridges & Brehme (7), in designing a gene-naming system for their own species.

Amongst the genes enumerated in the table there seem to be three cases of linkage. Hachinohe & Onishi (33) reported *Rw* and *l* linked with 31 per cent crossing over. Kerr & Laidlaw (39) stated that *rf* appeared to be closely linked with *bk* although the analysis was not completed. Mackensen (57) has found *h* and *ch* to be linked with 4.1 per cent crossing over.

Green (29) reports that the *i* and *s* mutants are homologous with certain mutants in *Drosophila*, *Habrobracon*, *Ephestia*, and *Bombyx*.

Radiation genetics in bees has been opened by Lee (44) in his study of the induction of dominant lethals in bee sperm cells. Drones were irradiated and then used to supply semen for inseminating queens. The primary measure of effect was viability of eggs laid in worker cells and presumably fertilized. At a dosage of 10,900 roentgens, over 99 per cent of the eggs failed to hatch.

The haploid origin of drones presents some features not common in genetics of higher plants and animals [population genetics in (17, 37, 42, 84, 85)]. It has been pointed out repeatedly that drones, genetically, are gametes. Ruttner (102) made an intensive study of drones produced by hybrid queens and emphasized the utility of such studies in analyses of polygenic inheritance. This and the related fact that all sperms from a drone are genetically identical except for mutations are likely to be utilized more extensively than they have been.

Bee Breeding

Variability in honey bees.—Variation among colonies of bees, as among individuals of other species, "is the raw material on which the breeder works" [Lush (47, p. 71)]. How much of the variation is due to heredity is of great importance. Without heritable variation there is no best genotype to perpetuate and further improve, and no poorest one to eliminate from a breeding population. Recent observations by Brother Adam (2, 4), as well as earlier observations by many other apiculturists, have established beyond

TABLE I

LIST OF MUTATIONS IN HONEY BEES

Symbol	Name of mutation	Effect on	When named and by whom		Citations
bk	brick	eye color	1953	Laidlaw, Green & Kerr	(39, 43)
c	cordovan	body pigment	1951	Mackensen	(43, 52, 129)
ch	chartreuse	eye color	1952	Rothenbuhler, Gowen & Park	(97, 99, 128)
ch^1	chartreuse-1	eye color	1953	Laidlaw, Green & Kerr	(39, 43)
ch^2	chartreuse-2	eye color	1953	Laidlaw, Green & Kerr	(39, 43)
ch^r	red	eye color	1953	Laidlaw, Green & Kerr	(39, 43)
cr	cream	eye color	1952	Rothenbuhler, Gowen & Park	(97, 99, 128)
D	Droopy	wings	1952	Rothenbuhler, Gowen & Park	(98, 99)
h	hairless	body hair	1957	Mackensen	(57)
i	ivory	eye color	1949	Rothenbuhler, Polhemus, Gowen & Park	(29, 98, 99, 100, 128)
i	ivory	eye color	1953	Laidlaw, Green & Kerr	(43)
l	lethal	viability	1953	Hachinohe & Onishi	(33)
m	modifier	chartreuse-1 eye color	1953	Laidlaw, Green & Kerr	(39, 43)
rf	reduced facet number	eyes	1956	Kerr & Laidlaw	(39)
Rw	Rudimental wing	wings	1953	Hachinohe & Onishi	(33)
S	Schwarzsuchtig	body hair	1940	Dreher	(18)
s	snow	eye color	1952	Rothenbuhler, Gowen & Park	(29, 98, 99, 128)
sh	short wing	wings	1956	Kerr & Laidlaw	(39)
—	ivory but always referred to as white	eye color	1931	Michailoff	(63)
—	haplo-viable homozygous lethal alleles, 11 different ones.	viability (suspected effect on sex)	1955	Mackensen	(42, 52, 54, 90, 95)

question that a tremendous amount of variation exists among races and strains of honey bees. This variation may be seen as differences in over-all apicultural merit; or, at a more basic level, it may be seen as differences in various characters of apicultural importance like honey-yielding ability, wintering ability, resistance to American foulbrood, etc.; or, at a third level, it may be seen as morphological, physiological, or behavioristic differences in the sub-characters which make up a given character. Comparisons between races and strains have been made at the various levels.

Park (76) conducted an extensive comparison between Carniolans, Caucasians, and Italians, with respect to characters of apicultural importance, and he cites references to some previous studies of like nature. More recently, in Germany, Braun (6) compared two races, and Reininghaus (87) compared six strains and races. Lunder (46) compared four races under Norwegian conditions. All of these studies revealed a great deal of variation in various characteristics of importance to the beekeeper.

Certain investigators have been intensely interested in measuring morphological characteristics of the various races of bees. No attempt is made here to review these investigations nor to assess their significance. A few selected citations will lead any interested investigator to this literature. Carlisle (16) studied forewing length, cubital index, number of wing hooks, tongue length, and hind leg length in about a dozen races of bees collected by Brother Adam. Okada, Sakai & Hasegawa (69) compared the Japanese honey bee with Caucasian, Italian, and Swiss bees. Sakai (105) made a similar study of several races and strains. Giavarini (23, 24) presented a study on the bees of Sicily. Hachinohe & Onishi (34) studied the effect of environmental factors, and particularly nutrition, on proboscis length. Goetze (25) considered the problem of selecting for proboscis length and cited several other publications. Temperature was shown by Soose (109) to have an effect on wing index and chitin color. Both Grout (30, 31) and Buchner (9) found that size of brood cell has some effect on size of bees reared in them. The abstracts of many other important papers in this general field have been published in the Apicultural Abstracts section of *Bee World*. *Archiv für Bienekunde* carries important literature, both papers and abstracts, in this field.

It is not particularly surprising, but nonetheless interesting, that variation in honey bees has been found to extend to their enzymes and their dances. Gontarski (26) reported enzymatic differences among the four races that he studied. Von Frisch & Lindauer (22), reviewing the works of Tschumi, of Hein, and of Baltzer, noted differences in the dances of various races. Every beekeeper knows there are colony differences in stinging propensities and these differences are more striking between races. Swarming tendencies in races of bees, like broodiness in breeds of chickens, vary tremendously. Honey bees show a rich development of behavior [Ribbands (88); von Frisch

(21); and Butler (10)]. There are many colony and race variations, for which a genetic basis may soon be found.

Efforts to obtain better bees seem to be classifiable into four categories: importation of stock; selection of females; selection of males and females with use of isolated mating yards; and selection of males and females with use of artificial insemination. There have been accomplishments under each of these.

Importation of stock.—About the mid-1800's great interest was aroused in possibilities for stock improvement through searching out superior indigenous races in the regions of their evolvement. Bees apparently were moved from one European, African, and Asiatic country to another, as well as to America and Australia [Phillips (83); Pellett (82); Rayment (86)]. Toward the end of the 19th century and in the early part of the 20th century, many different races of bees were brought to America and tried by beekeepers. Eventually the Italian race became established in place of the previously imported German or black bees. Caucasians and Carniolans were tried also and found considerable favor. The establishment of these races served to control wax moths and European foulbrood to which the German bees had been more or less susceptible. It must be concluded that importation of races, from about 1860 to perhaps 1910, served to provide better bees for beekeepers in this country.

Selection of females only.—Improvement to be gained by importation of races has a distinct ceiling. The undesirable characteristics of the race must be taken with the desirable ones, and the desirable ones are not improved. The notable progress made in animal and plant breeding [Lush (48); Muntzing (64)] as well as discoveries of principles of heredity during the early part of the 20th century stimulated interest in bee breeding, another avenue to improvement of bees. Due to lack of mating control, bee breeding was limited initially to selection of the best colonies in an apiary and the rearing of queens from them. Daughter queens were allowed to mate in free flight. Little or no control of male parentage can be assumed in this breeding system [Peer & Farrar (81)]. I know of no data that show what progress was made. It is commonly thought by beekeepers that unique and superior strains have been developed by this method.

Use of isolated mating yards.—The next step forward in bee breeding was the introduction of such control of male parentage as could be achieved in an isolated mating yard. Four examples of striking accomplishments through such mating control, all involving resistance to disease or parasites, will be presented.

One of these breeding programs started September 20, 1934, as a cooperative project among the Iowa Agricultural Experiment Station, the Iowa Agricultural Extension Service, and the *American Bee Journal* represented by O. W. Park, F. B. Paddock, and Frank C. Pellett respectively (72, 73). The first year of work involved bringing colonies of bees with an asserted resistance to American foulbrood (causative organism: *Bacillus larvae* White)

to one location at Atlantic, Iowa, for an experimental test. Caucasian, Carniolan, and Italian races were represented. Twenty-five supposedly resistant colonies and six supposedly nonresistant colonies were inoculated in early August, 1935, by inserting rectangular pieces of comb which contained at least 75 scales (dead larvae) of American foulbrood. All but one colony is known to have developed American foulbrood as a result of inoculation. By the end of September, 1935, the six control colonies still were infected as were eighteen of the twenty-five supposedly resistant colonies. Seven of the twenty-five, however, showed no visible symptoms of the disease. From these results and other observations (72, 73, 75), it was concluded that variation in resistance to American foulbrood exists in bees.

The next question to be answered was: "Is this resistance inheritable?" [Park (74); Park, Pellett, & Paddock (78, 79)]. A generation of offspring from the more resistant colonies was required to answer the question, and in order to facilitate the program, the cooperators obtained permission to move some of the tested stock into Texas. The Weslaco Substation of the Texas Agricultural Experiment Station became headquarters where Pellett and Park reared the new queens. An isolated mating station was established in the middle of a 25,000-acre citrus orchard, where it was felt that the virgin queens would be almost certain to mate with drones from the selected resistant colony.

The new generation was shipped to Iowa where twenty-seven colonies were inoculated in 1936 in the same manner as in 1935. Nine of the twenty-seven were apparently disease free by the end of the season. It was concluded that resistance is inheritable.

Other observations were made and several penetrating questions were posed in these early papers. It was found that all three races tested showed resistance. It was observed that bees reacted differently to comb inserts containing scales of American foulbrood and comb inserts that were disease-free. Eventually (80) it was established that breeding from colonies showing no disease following inoculation was more effective than breeding from recovery colonies.

In July, 1936, a cooperative project was organized among the states of Iowa, Texas, Wisconsin, and Wyoming, and the Division of Bee Culture of the U. S. Bureau of Entomology and Plant Quarantine (74, 78, 79). Under the new setup, the queens were reared by the Texas Agricultural Experiment Station and mated in isolated stations in the sandhills to the southeast of San Antonio. Substantial progress continued as indicated in Park, Pellett & Paddock (80), Park (77), Sturtevant (111, 112), and Mackensen & Roberts (59).

Table II presents some results of fifteen years of testing and breeding for resistance as summarized by Park [(71) and unpublished]. These results show what was accomplished and the rate of progress. Resistance was revealed by inoculating colonies with comb inserts containing 75 scales. In 1940 there seems to have been a drop in resistance. This was the first year

TABLE II

PROGRESS IN RAISING THE LEVEL OF RESISTANCE TO AMERICAN FOULBROOD BY BREEDING FROM SELECTED STOCK

Year	Number of colonies inoculated	At end of season:	
		Diseased	Not diseased
1935	25	72%	28%
1936	27	67%	33%
1937	114	29%	71%
1938	111	19%	81%
1939	148	8%	92%
1940	89	22%	78%
1941	59	14%	86%
1942	90	27%	73%
1943	89	24%	76%
1944	55	2%	98%
1945	66	2%	98%
1946	101	8%	92%
1947	37	19%	81%
1948	68	29%	71%
1949	62	2%	98%

that inoculation rectangles of comb were put into combs selected to contain eggs or hatching brood. Since only the very young brood is susceptible, this procedure amounted to a more severe inoculation. The drop in resistance in 1946, 1947, and 1948 was probably brought about, at least in part, by mismating. This period was one of transition from cooperative effort to individual effort by the Iowa Station alone, and new queen rearing and mating yards, in the south, were operated by new personnel.

TABLE III

LARVAE OBSERVED DEAD IN SEVERAL INSPECTIONS FOLLOWING INOCULATIONS OF THREE COLONIES—1945–1946

First inoculation		Second inculation		Third inoculation	
Scales given	Larvae dead	Scales given	Larvae dead	Scales given	Larvae dead
75–100	0–0*	75– 100	0– 0	4500–5500	1–66
75–100	0–1	2000–2500	0– 0		
75–100	0–1	2000–2500	0–10		

* First numeral represents larvae positively identified as dead of American foulbrood, and second numeral represents larvae dead but not positively identified as dead of American foulbrood.

During these years Park continued testing colonies with repeated inoculations and with very high doses of inoculum first mentioned in 1937 (74, 78, 79). Three colony responses are presented in Table III. For the very high dosages of scales, whole combs were given, and thousands of healthy bees emerged from the first cycle of brood in these combs. Such results indicate the high degree of resistance obtained. It was, in part, these results which stimulated Park's unwillingness to accept hygienic behavior as the sole mechanism of resistance. These results, Park's experience in this field, and a review of pertinent literature led eventually to a reappraisal of the problem of resistance to American foulbrood in bees. A new approach was formuated which involved development of both resistant and susceptible lines, and utilization of various techniques of inoculation and selection [Rothenbuhler & Thompson (101)]. The work of Park, *et al.* provides a notable example of what can be done in bee breeding. As such it is a sound foundation stone to support further building.

The second example is striking for its daring approach. Edward G. Brown (8), Sioux City, Iowa, long interested in better bees, has operated a wax-rendering plant for two or three decades. Every year he receives, for rendering, thousands of combs contaminated with American foulbrood. He always stacks these combs in the open so that his bees can remove the honey, and he does this regardless of the degree of infection in the combs. When some of his colonies are weakened by American foulbrood, they are robbed by their more populous neighbors. Naturally, only the more resistant colonies survive. New queens are reared and mated naturally in this yard. How much mismating occurs is unknown. No drugs are fed intentionally, but some drugs may have been obtained in the honey from colonies brought to him during recent years. Accession of drugs in this way would make his "natural selection" program less effective.

Over the years a high degree of resistance has been developed, but uniformity in resistance seems to be lacking. Inspection of his colonies reveals some with no symptoms of disease, but others show some larvae dead of American foulbrood. Colonies produced by ten queens of the Brown stock were tested at the Iowa Agricultural Experiment Station in 1954. Three were found to be highly resistant to an inoculation of 75 scales of American foulbrood; one was perhaps highly susceptible; and the other six fell between the extremes. From the best four of the ten queens, a highly resistant line has been developed, and the resistance level is still rising with each new generation (96).

The third example is taken from the history of American foulbrood in the Hawaiian Islands, as related by Eckert (19, 20) and Keck (36), and demonstrates the potency of natural selection on a larger scale. It seems that American foulbrood did not exist in the Islands, where apiculture flourished, until the early 1930's. There was then some inspection for the disease followed by burning of infected colonies. On the Molokai Ranch, Ltd. approximately 90 per cent of 2400 colonies were found to be infected and were destroyed. Beekeeping was almost completely neglected on this ranch for

ten years until 1949. At this time, inspection of 86 colonies showed 13 infected. Some of these apparently were free of disease later in the summer. The colonies produced by eight queens representing the Molokai Ranch stock were tested for resistance by giving them one or more combs containing scales of American foulbrood. Counts of diseased larvae seen in the broodnest are given by Eckert (19). It is almost certain that a high degree of resistance to American foulbrood had been developed in this stock between 1937 and 1949.

The last example of success with isolated mating stations comes from Brother Adam, who has utilized such stations for about three decades (1). He states that acarine disease, caused by the mite, *Acarapis woodi* (Rennie), is prevalent in the region of Buckfast Abbey in southwest England. He further states (1), "However, by means of careful selective breeding throughout a period of 20 years we have overcome the inherent susceptibility to this disease to such an extent that it practically never occurs."

Calvert (15) reared a new generation of queens from Brother Adam's stock, in northern Ireland, and mated some in isolation and others in a susceptible yard. Some of Calvert's colonies were requeened with the supposedly resistant stock, but others were kept as controls. No drugs or other treatments were given to any colony. The controls succumbed eventually and the supposedly resistant stock survived. Calvert summarizes (15),

> Beginning with infested stocks, and refraining from administering treatment of any kind, the experience of the past four years, has shown that it is possible, within a period of twelve months, to overcome the menace of acarine disease, by requeening colonies with a resistant strain of bees. The resistance characteristic is an inherited one and holds good in a first-cross.

Use of artificial insemination.—The introduction of artificial insemination cleared the way for rapid progress in bee improvment. A good technician with adequate help and favorable conditions can inseminate queens at the rate of ten per hour. Thus it is possible to inseminate a vast number of queens in a month's time, if this is desired. By use of artificial insemination dozens of distinct lines may be maintained in one apiary. For experimental purposes, matings may be obtained between two specific individuals. Without artificial insemination, development of inbred lines and controlled hybridization would be practically impossible.

Personnel of the United States Department of Agriculture, Division of Bee Culture, have been interested in development of hybrid bees for more than a decade. Some of the thinking behind this program, methods and techniques employed, and general discussion of results are presented by Roberts & Mackensen (90), Mackensen & Roberts (59), and Roberts (91). With regard to the success of the work, Mackensen & Roberts state, "Beekeepers who have obtained test queens have been favorably impressed by the superiority of certain double hybrids, which have produced as much as 50 per cent more honey than comparable commercial lines."

Cale (12, 13), and Cale & Gowen (14) presented studies on the problem of whether heterosis appears in egg laying rate of the queen and honey yielding performance of the colony. This work involved four inbred lines, their six nonreciprocal F_1's, and randomly selected, commercially available stock, as a control group. Inbred and F_1 queens were allowed to mate naturally in free flight. Experimental observations on all eleven genetic groups were made in six different apiaries. The six different hybrid combinations showed wide variation with respect to number of eggs laid per day by the queens, and pounds of honey produced by the colonies. In the cases of both characteristics, the hybrid performances were usually superior to the performances of the higher parental line involved, or of the commerical stock. In this experiment, inbreds exhibited both general and specific combining ability for oviposition rate and honey yield. Heterosis was clearly demonstrated for both characteristics and the promise of its further utilization in bee breeding is high.

Schwartz (107) was interested in the question of whether inbreeding depression would be found in certain body measurements of the bee. In one of his three experiments he utilized nine inbred lines and seventeen hybrid combinations. Measurements were made of body weight, length of scape of antenna, length of tibia 3, and length of radius vein of forewing. Some additional measurements were made in the first two experiments. Differences among lines were highly significant. The powerful technique of mixed-sperm mating was used in the study. Thus hybrid and inbred progeny developed in the same comb from two genetically different kinds of eggs laid at random by a queen. Significant depression due to inbreeding was not demonstrated, although Schwartz felt that small inbreeding depression might be found to exist. He stated, "The hybrids were usually intermediate in size between the parent inbreds though most measurements tended to be closer to those of the larger parent."

Recently, Mackensen (56) has reported finding a reduction in size of body parts appearing during the course of seven generations of inbreeding. Reduction, of the nine parts measured, varied from 1.7 per cent to 10.8 per cent. Whether there are genes affecting size of body parts in females that are not expressed in males is of interest [Kerr & Kerr (38); Schwartz (107)].

Opportunities for Further Work

In a species, such as *Apis mellifera*, which is so little explored genetically, opportunities for further research are almost unlimited. Some of these have been pointed out already, but others are worthy of mention.

There is a paucity of good marker genes having no deleterious effects. It seems that an inspection of a few thousand drones, with attention to hair and wing characteristics, might reveal new mutations. Radiation genetics could be helpful in this undertaking.

Genetic constitution of a plant or animal is one factor in determining its response to a pathogen or a pest [Gowen (27); Walker (118); Schneider

(67); Painter (70)]. Analyses of host-pathogen relationships have been carried further in the case of American foulbrood than any other bee disease. With the accumulation of results, remaining problems seem to come into focus. A sound start has been made on the division of over-all colony resistance into its component subcharacters, i.e., the individual mechanisms of resistance [Park (72, 73); Woodrow (124); Woodrow & Holst (125); Sturtevant & Revell (113); Thompson (115); Rothenbuhler & Thompson (101); Thompson & Rothenbuhler (116); and Lewis (45)]. Opportunities in this field, nevertheless, are far from exhausted. Determination of the genetic basis of each mechanism of resistance appears to present important problems and such work is in progress in our laboratory. Further studies on resistance to European foulbrood, acarine disease, and nosema disease are desirable.

In his consideration of the aims of breeding, Brother Adam (3) lists almost two dozen apiculturally desirable characteristics in which bees vary. The more that is known about the heredity of each desirable characteristic, the easier it will be to breed a bee possessing all of them. The task would be easiest if each gene involved were known, but lacking this, any information will be helpful. The tremendous opportunities herein are obvious.

A review of literature has shown that the breeding of a bee specifically for pollination purposes is a promising possibility [Rothenbuhler, Gowen & Park (93)]. Particularly stimulating is the work of Akerberg & Lesins (5) who reported that two colonies belonging to two different races varied widely in whether or not they tripped alfalfa. Even though there is interest in breeding bees for pollination in Canada and Norway, no results have been reported.

One of the most promising procedures for improvement of honey bees is hybridization of selected inbred lines. Yet by comparison with maize [Sprague (110)], almost nothing is known about development, testing, and utilization of inbred lines of bees. Gamete selection is particularly accessible, and its evaluation might be important. Various types of recurrent selection ought to be evaluated. The genetic basis of heterosis, yet unknown [Gowen (28)], could well be the subject of investigations by bee breeders. It is permissible to hope that through such studies honey bees will contribute to genetic theory, which would be a rare accomplishment for them since the time of Dzierzon.

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THE PHYLOGENY OF THE PANORPOID ORDERS[1]

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Of the most significant advances made during the past two decades or so to our understanding of the phylogeny of the Insecta and other classes of the subphylum Antennata, recognition of the following could be cited: (*a*) the polyphyletic nature of the old groups Myriapoda and Hexapoda; (*b*) the extreme isolation of the class Collembola and their lack of any close resemblance to the Insecta; (*c*) the close relationship that exists between the Symphyla, Entotrophi (= Diplura), and Insecta, especially since the demonstration by Tiegs of the secondary nature of the progoneate condition of the Symphyla; (*d*) the Protura as a class distinct from the Insecta; (*e*) the very great differences that exist between the Ephemeroptera and other pterygote insects, including the Odonata; (*f*) the isolation of the Dictyoptera (cockroaches, mantids) from the old order Orthoptera and the relation of the Isoptera and Zoraptera with the Dictyoptera: (*g*) the monophyletic origin of the Endopterygota; and (*h*) the close relation between the Megaloptera-Neuroptera and the Coleoptera-Strepsiptera.

The number of papers that have been published on the relations of the orders of insects is great, and no year passes without further addition. With very few notable exceptions, however, it must be admitted that these papers consist of no more than a kind of juggling in which only a few of the facts of anatomy available in the literature are used, and, more often than not, it is only too clear that the authors have no intimate personal knowledge of the structure of the groups of which they write.

In the space available here no more will be attempted than a discussion of the relations of the orders of the superorder Panorpoidea, the "panorpoid complex" of many. For the convenience of the reader, the orders, suborders, and some other higher categories of the Panorpoidea are listed at the end of this article, on page 204-5.

Again owing to limitations of space, all stages of the insects cannot be dealt with adequately. The discussion is based largely upon the immature stages. This choice is not made because it is thought that they reveal phylogenetic relationships more clearly than do the adults, but because much less is known about the larvae. Their structure makes clear certain relationships previously unsuspected and precludes some derivations once thought possible on the basis of the better known adult structures. The first and largest section of this paper consists of a review of the anatomy of the larvae. Some structures which do not appear to contribute to a knowledge of the relations

[1] The survey of the literature pertaining to this review was completed in March, 1957.

of the orders, e.g., the mandibles, are omitted. Statements of fact for which no authority is quoted are taken from my unpublished work on the larvae of the superorder.

COMPARATIVE ANATOMY OF PANORPOID LARVAE

Cranium

Many morphologists have believed that the various lines and grooves present on the cranium delimit the primary segments of which the head is composed. But the secretion of the cuticle always occurs after the formation of a definitive epidermis that itself bears little or no trace of the metamerism that may be deduced from the coelomic sacs, nervous system, and paired appendages. The persistence of the belief that the various sutures of the cranium reflected its metamerism is curious indeed when we note that when a species has two stages that live in very different environments, the sutures of the head are often very dissimilar; and this fact of itself is evidence that in at least one of the two stages the sutures are not related to the metamerism, which is the same in both stages.

It has been shown by DuPorte (21, 23), Snodgrass (58), and Hinton (38) that the more stable of the cranial sutures have a functional significance and do not delimit homologous areas in the different orders of insects. These papers destroy the premises on which the work of Ferris (25 to 28), Evans (24), and others is based. The studies of Ferris (29) and Henry (34) on the segmentation of the arthropod head are based on the topography of the definitive nervous system. The reader is referred to Manton (48) for an estimate of this work by Ferris and his school.

The grooves and lines on the cranium have a functional significance: some are lines of weakness along which the cranium splits when the old cuticle is shed; others are simply the external marks of internal strengthening ridges formed along lines of stress; and still others are the result of an infolding of the cuticle by means of which ridges are developed which function as points of attachment for certain muscles or serve to strengthen the head, or both. Although it can be shown clearly that nearly all the sutures of the cranium of larval and adult insects are not related to the primary segmentation of the head, it does not follow that these lines and grooves are not of great value in assessing relationships between families and orders. The form of these lines and grooves in different groups at once reveals the fact that some of them have persisted with little change over immense periods of time. For this reason, they may be supposed to reflect certain aspects of the more stable features of the relation between the insect and its environment or be connected with postembryonic developmental processes that are common to most insects. Others show significant differences at the family or even generic or specific levels, and the latter may thus be supposed to reflect the more readily modified aspects of the relation between the insect and its environment.

On the dorsal aspect of the cranium of most larval insects there is a ⅄-

shaped line or suture, generally known as the epicranial suture. The stem or coronal part of this suture is a continuation of the median longitudinal line present on the thorax and often on one or more abdominal segments. The epicranial suture, called the cleavage line (58), is a preformed line of weakness along which the cranium splits when the cuticle is shed. The coronal suture is often irregular. This irregularity is particularly noticeable in some trichopterous larvae, e.g., *Polycentropus*, in which the adductor muscles of the right and left mandibles arise very close to the median line. These muscles differ both in number and disposition, and if the coronal line is to be formed between the muscle origins, as it always appears to be, the irregularities of its course are imposed by the asymmetry of the muscle origins.

Snodgrass (58) claimed that in all larval insects the arms of the cleavage line (frontal sutures) extend through the cranial areas that intervene between the attachments of the mandibular muscles and those of the facial muscles. In both Trichoptera and Lepidoptera, however, one of the pair of muscles that are inserted on the dorsal wall of the pharynx and pass within the loop formed by the cerebral connectives of the frontal ganglion, arises laterad from the arms of the cleavage line near the point of origin of the cranial retractors of the antenna (38). More recently, Chiswell (8) has shown that, whereas in some Tipulinae [*Dictenidia bimaculata* (Linnaeus)] all of the facial muscles arise between the arms of the cleavage line, in other Tipulinae (*Tipula* spp.) the cibarial dilator muscles, the anterior pharyngeal dilator muscles, and the oral arm retractor muscles all arise laterad from the arms of the cleavage line. Today as in the past, insufficient attention to the functional significance of the sutures and other features of the cranium results in overestimates of their value for purposes of homology.

In the Zeugloptera, Trichoptera, Boreidae, Mecoptera,[2] Siphonaptera, and in some primitive Nematocera (e.g., Bibionidae) the cleavage line is of the usual ⅄-shaped form. The stem may be short or long, and there is some difference in the course of the arms towards the anterior margin. Such differences may be found within a single order. It may be noted here that at ecdysis sometimes only one arm splits, e.g., in the specimens of *Micropteryx* seen only the right arm of the cleavage line is split by the pupa. In a few Lepidoptera cleavage lines are distinct in the first instar, e.g., *Oncopera* (Hepialidae), but in the great majority cleavage lines do not appear until the third or fourth instar, the cranium being shed unsplit in earlier moults (38). The cranial cleavage line of the Lepidoptera is unusual in that it is always Λ-shaped: the two arms are never united on the cranium to form a coronal stem. When the apex of the Λ is some distance in front of the hind margin, the median adfrontal suture appears at first sight to be the coronal suture, but the cleavage lines are separately continued to the hind margin beneath the surface and are not visible externally. They are continued beneath the

[2] In this section on comparative anatomy, Mecoptera will refer to the Mecoptera exclusive of the Boreidae, i.e., the Panorpidae, Choristidae, and Bittacidae. For further discussion of the status of the Boreidae see p. 203.

surface on the sides of the stem of the median inflexed ⅄-shaped strengthening ridge, as shown by Hinton (38).

On the ventral surface surface of the cranium of many endopterygote larvae cleavage lines also occur (38), and those of some larvae have been called gular sutures. When the cranium is heavily sclerotised, it not only splits along the dorsal cleavage line at ecdysis but also splits along one or more ventral lines. The ventral lines that split open at ecydsis are preformed lines of weakness which are morphologically and functionally comparable with the dorsal cleavage lines, and they may be called the ventral cleavage lines. The ventral cleavage lines are by no means so constant a feature of endopterygote larvae as are the dorsal cleavage lines; they are frequently absent.

There is no apparent connection between the position of the posterior tentorial pits, often called gular pits, and the course taken by the ventral cleavage lines, just as the position of the anterior tentorial pits is unrelated to the course of the dorsal cleavage lines. The ventral cleavage lines are nearly always described by morphologists as the gular sutures, and, when a single median line is present, it is said that the gular sutures are fused. Where lines representing internal strengthening ridges are present, they are frequently described as gular sutures, so that in endopterygote larvae lines which are morphologically and functionally dissimilar are customarily described as gular sutures. Moreover, the ventral cleavage lines of the larva are homologised with the "gula sutures" or lines of the strengthening ridges of the adult, which is absurd.

In the Trichoptera the ventral cleavage system may be a straight line extending from the occipital foramen to the submentum, two parallel lines, or a ⅄-shaped line. When the head capsule is shed, one or both of the anterior arms of the ⅄-shaped line may be split. The lines of weakness on the ventral cranial areas appear to be functional even when ventral splitting does not occur. In such instances they function as hinges that facilitate the outward opening of the two halves of the cranium when the dorsal cleavage line has split.

In many panorpoid larvae the ventral region of the head is membranous, e.g., most caterpillars, and when the cranium is split at ecdysis the ventral membranous region serves as a hinge but does not itself split. In a few caterpillars, however, e.g., *Acrolophus* (Tineidae), in which the ventral cranial area is heavily sclerotised, a median ventral cleavage line extends from the base of the postmentum to the occipital foramen. In many Hesperidae, e.g., *Celaenorrhinus* spp. the ventral cranium is heavily sclerotised and there are three lines of weakness, a median line and one on each side laterad from but very close to the hypostomal ridge. The left lateroventral line was split at ecdysis in the species examined, and in one the median line was also split.

In all lepidopterous larvae part of the dorsal cranium is inflexed and forms a large ⅄-shaped strengthening ridge, the adfrontal ridge, the evolution of which is probably connected with the structural weakness of a head with so large an occipital foramen. The structure of this ridge has recently

been described (38), and the details need not be repeated here. It is interesting to note that in some Mecoptera such as *Panorpa*, which also have a very large occipital foramen, there is a slight thickening of the cuticle in a position comparable to the arms of the adfrontal ridge of caterpillars.

In larval Panorpoidea the clypeus is fused to the frontal region of the head. The area between the cleavage lines may be called the frontoclypeal apotome. The clypeal area may therefore be distinguished from the frontal only by the distribution of the muscle origins: the cibarial dilators arise on the clypeus, and the muscles that pass within the loop formed by the cerebral connectives of the frontal ganglion arise on the frontal region. But important exceptions to this rule have already been noted, and in caterpillars some of the mandibular muscles arise within the area enclosed by the arms of the dorsal cleavage line (38). The larvae of the Mecoptera (excluding Boreidae) are exceptional in that there is a very distinct transverse suture between the frontal region of the head and the clypeus. This suture is the external mark of a well developed internal ridge. Its position seems to correspond to that of the frontoclypeal suture of primitive exopterygotes.

In all panorpoid larvae except the higher Diptera the tentorium consists of posterior and anterior arms and a transverse bridge. The posterior arms always arise on the postoccipital ridge or very near it. The points of origin of the anterior arms differ considerably. In the Lepidoptera they arise on the adfrontal area far behind the bases of the antennae, in Zeugloptera just mesad from the antennae, and in fleas between the antennae and mandibles. In the Trichoptera they usually arise on the frontoclypeal apotome adjacent to the mesal sinuation of the frontal arms of the cleavage line, but in a few, e.g., most Hydropsychidae, they arise some distance mesad from the cleavage line. In the Zeugloptera, Boreidae, and Mecoptera the tentorial bridge is short and thick and not far above the postoccipital ridge. In the Lepidoptera it is slender, and in the Trichoptera and Siphonaptera it is very slender indeed and has previously been overlooked except in fleas, where it was first correctly described by Sharif (54). In these orders, the common duct of the labial glands enters the head beneath the bridge and the gut above the bridge. The tentorium is independently lost in a number of Diptera-Nematocera. For instance, it is said to be absent in the Psychodidae. In the Simuliidae and Tendipedidae only the posterior pits are evident (12), and in the Stratiomyidae only the anterior arms are present (12). In the Bibionidae and Culicidae a tentorial bridge is said to be absent (12). I have verified the existence of a tentorial bridge in the Bibionidae (*Bibio marci* Linnaeus), where it is very slender. It seems hardly likely that the bridge is absent in the Californian species of *Bibio* as Cook (12) claims. The absence of a tentorial bridge in the Culicidae and other Diptera in which the arms are complete therefore requires confirmation.

Labrum

The labrum is well developed in all larvae of the Panorpoidea except those of some Diptera. In the more specialized Diptera, the labrum may be

greatly reduced; and in the higher Brachycera it is not recognizable as a distinct sclerite. Amongst the more primitive exopterygotes, as amongst the less specialized larvae of the Neuropteroidea and Hymenoptera, the labrum is provided with both median and lateral retractor muscles. The labral muscles arise on the frontal region of the cranium. Within the Panorpoidea, the larvae of the Zeugloptera and Trichoptera possess both groups of retractors. The other panorpoid orders have a more specialized labral musculature: in the Lepidoptera the median retractors are lost, whereas in the Boreidae, Mecoptera, and Siphonaptera, it is the lateral retractors that are lost. In the Lepidoptera muscles inserted in what I consider to be the palatal membrane are claimed to be median labral retractors by DuPorte (22).

The postero-lateral angles of the labrum are normally produced posteriorly and slightly ventrally to form sclerotized rods called tormae. When lateral retractors are present, they are always inserted on the tormae, and these muscles are therefore frequently called tormal muscles. In some larvae lacking lateral retractors, e.g., Boreidae, Panorpidae (*Panorpa*), Choristidae (*Chorista*), and Bittacidae (*Bittacus*, *Harpobittacus*), the tormae are well developed, and in *Bittacus* extend downwards and become united with the dorsal surface of the palatal membrane. The only species of Mecoptera examined in which the tormae were not well developed was *Apterobittacus apterus* (McLachan).

Of the Trichoptera examined (Rhyacophilidae, Polycentropidae, Limnephilidae, Helicopsychidae, Hydropsychidae), the single hydropsychid had, besides the usual lateral retractors, a slender muscle arising on the clypeus and inserted on the extreme apex of the torma. It is possible that the latter muscle is one of the cibarial muscles that has shifted its insertion.

In the Zeugloptera (*Micropteryx*) there is a submedian retractor on each side inserted on the posterior margin of the labrum half way between the median and lateral retractor. It has not yet been possible to determine the origin of these submedian retractors, but their length suggests that they arise on the clypeus; and it is possible that they are homologues of the anterior cibarial muscles, the insertions of which have become shifted from the cibarial membrane to the labrum. Submedian labral retractors are not found elsewhere in the Panorpoidea except possibly some Diptera, where they may be cibarial muscles that have shifted their insertions anteriorly. In the Siphonaptera one of the cibarial muscles inserted in the palatal membrane has been called the posterior labral retractor (54).

The labral muscles are very variable in the Diptera, and in many Brachycera are lacking. The Diptera belong to the section of the Panorpoidea that has lost the lateral retractors but retains the median retractors; and they are the most specialized order of that section. The median retractors of the Tendipedidae are called messorials by Cook (12) as are their apparent homologues in the Bibionidae. According to Cook, the messorials are cibarial muscles that have shifted their insertions anteriorly. If Cook be correct, we have to suppose that the Diptera not only lost the median retractors but

subsequently acquired a new set of median retractors by modification of cibarial muscles already present. In *Tipula* there is a single pair of retractors that are probably median retractors rather than approximated lateral retractors. In other Nematocera homologues of the messorials of Cook are present, but lateral retractors are absent. Cook does not produce any real evidence for his statement that the muscles he calls messorials are in fact cibarial muscles and not homologues of the median retractors of the Mecoptera. In the Culicidae and Simuliidae lateral labral retractors are described as messorials, whereas the median muscles that appear to correspond to his messorials of the Tendipedidae are described as anterior palatal muscles. I suspect that the common ancestor of recent Diptera retained only the median retractors, and that where lateral retractors are present they are in fact cibarial muscles that have shifted their insertions on to the tormae. As previously mentioned, muscles that have secondarily shifted their insertions on to the labrum (or are new muscles?) are found in the Hydropsychidae and Micropterygidae, in both of which families the primitive lateral and median retractors are retained.

When the labrum is well developed, it can usually be retracted to a greater or lesser extent beneath the clypeus. Retraction is accompanied by an infolding of the membranous region of the anteclypeus. The anteclypeus is frequently provided with fine anteclypeal muscles inserted on its anterior membranous margin. These muscles assist in the inward folding of the membranous anteclypeus. Two to four pairs of anteclypeal muscles have been found in some but not all species of Trichoptera and Lepidoptera examined. Cook (9, p. 16) says, "The anteclypeus, whatever its morphological origin, may readily be distinguished by the fact that it never bears muscle origins or insertions."

Compressor muscles are a primitive feature of the pterygote labrum: such muscles are of general occurrence among both exopterygotes and endopterygotes. Within the Panorpoidea labral compressors are absent only in some Diptera. Cook (11, p. 71) thinks that the Tendipedidae are unique amongst Diptera in retaining labral compressors, but I have found these muscles also in the Tipulidae and Fungivoridae (*Ceroplatus*, *Arachnocampa*). In the Trichoptera there may be six pairs of labral compressors (some Polycentropidae), or fewer pairs, or more than six pairs (some Hydropsychidae). In the Lepidoptera, where they have been overlooked by Snodgrass (56, 57), Das (19), Cook (9), and others, there are usually two to six pairs. In *Cossus cossus* Linnaeus, however, there appears to be only one pair which is unusual in being inserted slightly behind the apices of the tormae in the palatal membrane some distance behind the postero-dorsal margin of the labrum on which it arises.

Eyes

Apparently all flea larvae lack eyes. The eyes of the Zeugloptera, Trichoptera, Lepidoptera, and Diptera are lateral ocelli. These are special larval

organs. They are not precursors of the imaginal eyes nor do they resemble them in structure (57). The number of ocelli varies, and in the larger orders some or many species may lack ocelli. The maximum number on each side is five in Zeugloptera, seven in the Trichoptera, and six in the Lepidoptera. The lateral eyes of the Mecoptera are reduced compound eyes, and there are no important differences in structure between the ommatidia of the larval and adult eyes (4). The number of ommatidia in each eye varies considerably, e.g., 30 to 35 in species of *Panorpa* and 16 in *Nannochorista*. *Boreus* has three facets on each side of the head. The structural details of these are unknown, but it seems unlikely that they are ommatidia. It may be noted here that mecopterous larvae are the only endopterygote larvae known to have compound eyes.

Antennae

Owing to the simplicity of its basic structure, the larval antenna seems to be of little value in assessing relationships at an ordinal level. No muscles arise in the first segment, as in adult pterygotes. Two and occasionally more groups of fibres are inserted on the basal segment. In the Zeugloptera, Lepidoptera, Mecoptera, and many Diptera these arise on the cranium. In the Culicidae they arise on the anterior arm of the tentorium (12), as does one group of fibres in the Siphonaptera (54). Antennal muscles are lacking in the Trichoptera, in such Diptera as have much reduced antennae, and possibly in some leaf-mining caterpillars with much reduced antennae. The point of origin of the antennal muscles of the Boreidae is unknown.

Maxillae

The maxilla of the order Zeugloptera (*Micropteryx*, *Sabatinca*) is less specialized than that of any other recent order of the Panorpoidea; the cardo is well developed and the lacinia and galea are separate and distinct. In all other orders the cardo is either fused to the stipes (Mecoptera, Siphonaptera, Diptera), or, if it is not so fused, the maxillary lobe is undivided (Trichoptera, Lepidoptera, Boreidae). In the Zeugloptera, as in other panorpoid orders, the stipes is transversely divided. The proximal segment of the stipes is here called the basistipes and the distal segment the dististipes.

The subdivision of the stipes is a primitive feature of the Panorpoidea, and it is so divided in all except the more specialized Diptera. When the cardo is distinct and not fused to the basistipes, the dististipes has been called the palpifer. For instance, the dististipes of the Trichoptera has been called the palpifer by Crampton (16). However, in many Trichoptera the dististipes is particularly large and sharply delimited. It bears both the palp and the maxillary lobe; it is in no sense a basal segment of the palp but is often as long and nearly as broad as the basistipes. The palpifer is defined by Snodgrass (57, p. 156) as, "A lobe of the maxillary stipes bearing the palpus." This definition would seem to preclude the use of the term palpifer for the segment of the stipes here called the dististipes, but whether or not the distal

part of the stipes is called the palpifer or dististipes is, within the Panorpoidea, a matter of form and not of content.

Failure to recognize the fact that the stipes is subdivided in primitive forms of all recent orders of the Panorpoidea has not only resulted in the identification of the dististipes as the palpifer but has had consequences of more serious import: in the Panorpoidea in which the cardo has become fused to the basistipes, the combined structure, which may be called the cardostipes, has almost without exception been identified as the cardo and the dististipes as the stipes. For instance, the cardo+basistipes of *Bibio* is called the cardo and the dististipes is called the stipes by Imms (44) and Cook (12). The parts of the maxilla of the Trichoceridae, Anisopodidae, Ptychopteridae, and Psychodidae have been similarly misidentified by Anthon (1, 2). The maxilla of *Bibio* is very similar to that of *Panorpa*, and in the Bibionidae as well as other Nematocera (Simuliidae, Tipulidae, and others) the cardostipes is distinct from the dististipes. But within the Nematocera a fusion of the cardostipes with the dististipes occurs, e.g. in the Culicidae. Of the maxilla of the latter family Cook (10, p. 50) says, "The cardo and all of its muscles have been lost and the stipes has developed secondary articulations with the cranial margin." In the more specialized Diptera, not only is there a fusion of cardostipes and dististipes, but these become fused in varying degree with the mandibles (5, 12, 49). The mouth hooks of the Cyclorrhapha are modified mandibles (47). In the Siphonaptera the area of the cranium immediately behind the cardostipes has been called the cardo by Sikes (55).

Attention has been paid to the musculature of the maxilla of lepidopterous larvae by Snodgrass (56, 57) and Das (19). According to Snodgrass, the dististipes and the lobe borne on its apex are all parts of the lacinia. Of these he says (56, p. 140),

> The insertion of the three muscles on a single sclerite in the base of the maxillary lobe [my dististipes] leaves no evidence to indicate the presence of a galea, and suggests that the lobe is the lacinia alone, complicated in form by the development of large sensory papillae. Certainly the musculature of the lobe shows that none of the papillae can be a palpal rudiment.

Of the same maxilla, Das (19, p. 55) claims that the dististipes (subdivided in the caterpillars he has seen) is the basal segment of the maxillary palp of which he says,

> The insertion of the palpal muscles at the base of the structure shows that it is the maxillary palpus, and the lobe borne by the second segment of the palpus cannot be the galea as it was supposed to be by Crampton (1921). For the galea could not be borne by a distal segment of the palpus, unless it is proximally fused with the two basal segments of the palpus, which is improbable.

The assumption explicit in the interpretations of Snodgrass and Das is that a palp must have muscles inserted at least in its basal segment. Both writers are unaware of the fact that muscles are never inserted in either the maxillary

or labial palpi of any larvae of the Panorpoidea: muscle origins and insertions are guides to homology; they are not unquestionable proofs of homology.

In the Lepidoptera the cardo is often a single sclerite but may consist of two very distinct sclerites. The stipes is always transversely divided. In the Dacnonypha (*Eriocrania*) and in the Hepialidae and Tischeriidae the dististipes is not divided. In some Monotrysia (*Adela*), however, it is divided into two distinct sclerites as it is in all (?) Ditrysia. It is possible that some exceptions will be found in the diplotreme leaf-miners, of which I have seen very few.

A brief summary of the musculature of the maxilla of larval Panorpoidea is as follows:

Cranial promotor of cardo.—Absent in all Panorpoidea. Amongst endopterygote insects a cranial promotor of the cardo is present in the Neuropteroidea (Megaloptera, and most but not all Coleoptera) and in the Hymenopteroidea (at least some sawflies).

Tentorial adductors of cardo.—Present in the Zeugloptera, Trichoptera, Lepidoptera, and Boreidae. These muscles are absent in the Mecoptera (Panorpidae, Choristidae, Bittacidae), Siphonaptera, and Diptera, all of which have the cardo fused to the basistipes, or they have become tentorial adductors of the cardostipes.

In the Trichoptera examined, the tentorial adductor of the cardo is a single large muscle that arises on the anterior part of the tentorium and is here contiguous with the tentorial adductor of the stipes. In *Hepialus* there is a single tentorial adductor, but in other Monotrysia, e.g. *Adela*, there are two tentorial adductors, as in all Ditrysia I have examined. Snodgrass (56) claims that in some Phalaenidae there are three tentorial adductors. In the Boreidae there are two tentorial adductors.

Tentorial adductors of basistipes.—These muscles are present in all Panorpoidea except the Diptera. In the Trichoptera there are one or two, in the Lepidoptera generally three but sometimes two, three in the Boreidae, and two in both the Panorpidae and Bittacidae.

In the Siphonaptera a sclerotised bar, that is continuous with the mesal stipital ridge, extends posteriorly considerably beyond the posterior margin of the cardostipes so that its apex lies some distance beneath the sclerotised bar on which the mouth-angle retractor is inserted. A muscle that is apparently homologous to a stipital adductor is inserted on the apex of the stipital apodeme and arises just in front of the tentorium. Another muscle is inserted on the dorsal apex of the stipital apodeme, but this is attached to the sclerotised bar on which the mouth-angle retractor is inserted. Sharif (54) believes that the latter is one of the ventral pharyngeal muscles, but it is possible that further work may show it to be one of the stipital adductors that has shifted its origin.

In the Trichoptera, according to Das (19), the tentorial adductors of the stipes are inserted on the mesal edge of the stipes in *Anabolia nervosa* Leach (Limnephilidae) and in some Hydropsychidae, Hydroptilidae, and Philo-

potamidae. In the Hydroptilidae and Helicopsychidae and in some of the Limnephilidae which I have examined, the sides of the mentum and stipes are more or less completely fused where the one or two tentorial adductors are inserted, so that it is not clear to me on which of these sclerites the muscles are actually inserted. In at least one limnephilid (*Limnephilus lunatus* Curtis), however, the adductors are inserted on a small sclerite in the membrane between the sclerotised sides of the mentum and stipes. It might be supposed that this sclerite is therefore part of the stipes but for the fact that in the Polycentropidae and Rhyacophilidae (two species of *Rhyacophila* and one belonging to an unidentified genus) the tentorial adductors are actually inserted on the sides of the mentum and not on the stipes. This remarkable shift of the tentorial adductors of the stipes from the first to the second maxilla was verified in at least a dozen specimens of various species of Polycentropidae and Rhyacophilidae. Since the primitive insertion of the tentorial adductor of the stipes is on the stipes, it is of interest to note that an insertion which can only be regarded as highly specialised occurs in the Rhyacophilidae, which are by many regarded as the most primitive of recent Trichoptera.

Cranial flexor of dististipes.—This is the homologue of the cranial flexor of the lacinia of more primitive endopterygote larvae. It is present in all Panorpoidea except the Lepidoptera[3] and the more specialised Diptera. In the Boreidae, Trichoptera, and primitive Diptera, this muscle is inserted on the dististipes. In the Zeugloptera it also appears to be inserted on the dististipes, but of this I am not quite certain. In the Panorpidae, Choristidae, Bittacidae, and Siphonaptera it is inserted on the basistipes, which in these groups is fused to the cardo, and the muscle must therefore be called the cranial flexor of the cardostipes.

In the Trichoptera the cranial flexor of the dististipes has its origin on the postoccipital ridge slightly dorsal to the cranial extensor of the dististipes and is inserted on the apex of the long sclerotised projection from the inner angle of the dististipes. There seems to be little doubt that this muscle is the homologue of the cranial flexor of the lacinia present in less specialised endopterygote larvae and in primitive exopterygota. For instance, in some beetles, such as *Ptinus* (19, pl. 6, fig. 34), that have an undivided stipes, the cranial flexor of the lacinia is inserted at approximately the same level of the stipes as in the Trichoptera.

Cranial extensor of dististipes.—This is the homologue of the cranial flexor of the stipes of the Neuropteroidea and Hymenoptera. It is present in all Panorpoidea except specialised Diptera. It always arises on the postoccipital ridge or on the cranium in front of this ridge.

In the Trichoptera the cranial extensor of the dististipes is inserted on the

[3] Snodgrass (57, p. 304) claims that the maxillary musculature of trichopterous and lepidopterous larvae is the same, but he has overlooked the loss of the cranial flexor of the dististipes in caterpillars.

outer angle of the dististipes and has its origin on the postoccipital ridge slightly mesad from the posterior end of the tentorium. In the Lepidoptera there is a muscle that has a similar origin and insertion and can therefore be considered to be homologous. Both Snodgrass (56) and Das (19) agree in believing that this muscle of the Lepidoptera has no homologue in any other order. Snodgrass believes that it is inserted on a basal sclerite of the lacinia and Das that it is inserted on the basal segment of the maxillary palp. The fact that it is actually inserted on the dististipes and that it has its origin on the cranium seems to show that it is a homologue of the muscle known as the cranial flexor of the stipes in the Mecoptera and some primitive Nematocera (Bibionidae, Tipulidae). In view of the fact that it is antagonistic to the cranial flexor of the dististipes (homologue of the cranial muscle of the lacinia), it may be called the cranial extensor of the dististipes.

In *Panorpa* there is a cranial extensor of the dististipes which is called the cranial flexor of the stipes by Das (19) and the cranial flexor of the palp by both Bierbrodt (4) and Imms (44). I have examined larvae of *Chorista*, *Bittacus*, and several species of *Panorpa*, including *P. communis* Linnaeus, and I find that without exception this muscle is inserted on a small sclerite of the dististipes below the outer base of the galea. In my opinion, this sclerite is on the oral membranous part of the dististipes. The segment that I consider to be the dististipes is regarded by Das (19), Bierbrodt (4), and Imms (44) as the basal segment of the maxillary palp. On the ventral or outer face of the maxilla it is clear that the sclerotised part of this segment embraces the base of the maxillary lobe (galea plus lacinia) as well as the first true segment of the palp. Furthermore, the distribution of the innervated setae agrees with my interpretation: there are two on the basistipes (in *Panorpa* fused with the cardo) and one on the dististipes precisely as in the primitive Trichoptera and Lepidoptera.

In the Panorpidae, Choristidae, and Bittacidae the cranial extensor of the dististipes consists of no less than six separate muscles that are inserted on the apodeme that extends posteriorly from the dististipes. In some primitive Diptera, e.g., Bibionidae and Tipulidae, the cranial extensor of the dististipes consists of three muscles.

Stipital extensor of dististipes.—This is probably the homologue of the levator of the maxillary palp, but it is never inserted in the palp in the Panorpoidea. It is present in all except the Diptera.

In the Trichoptera and Lepidoptera it is inserted on the outer angle of the hind margin of the dististipes and arises on the inner angle of the hind margin of the basistipes.

In *Panorpa* the stipital extensor of the dististipes has been described as the extensor of the maxillary palp by Bierbrodt (4) and Imms (44), both of whom have mistaken the dististipes for the basal segment of the maxillary palp. In the Siphonaptera the stipital extensor is a large muscle inserted on the postero-lateral angle of the dististipes and arising on the cardostipital apodeme at a point some distance behind the postero-ventral margin of the

cardostipital sclerite. Sharif (54, p. 478) has described a small muscle inserted on the basal segment of the maxillary palp of *Nosopsyllus*, but I think that there can be little doubt that he has mistaken a portion of the large palpal nerve for a muscle. I have examined the palp of several genera of fleas (*Ceratophyllus*, *Xenopsylla*, *Hystrichopsylla*), but I have found no trace of such a muscle.

Stipital flexor of dististipes.—This is probably the homologue of the depressor (or flexor) of the maxillary palp of more primitive endopterygotes such as the Megaloptera and Coleoptera. A stipital flexor of the dististipes is present in all Panorpoidea that I have examined except the Diptera, Siphonaptera, and *Bittacus*.

In the Trichoptera the stipital flexor of the dististipes is inserted on the inner side of the hind margin laterad from the insertion of the cranial flexor and always passes beneath the extensor. Its origin is near the middle of the hind margin of the basistipes. Its origin and insertion are similar in the Lepidoptera, but, as this order lacks the cranial flexor of the dististipes, the stipital flexor is the only muscle inserted on the inner hind margin of the dististipes.

In the Panorpidae and Choristidae there are two to four groups of flexor fibres parallel to each other. In *Panorpa* these have been overlooked by Bierbrodt (4) and in the same insect have been described as flexors of the galea by Imms (44). A flexor of the galea is, however, absent in all members of the Panorpoidea. I have been unable to find a stipital flexor of the dististipes in *Bittacus*.

In the Siphonaptera the stipital flexor may have become a component of the extensor group of fibres. In the Boreidae the homologue of the flexor is inserted very close to the extensor on the outer hind margin of the dististipes. It arises near the inner hind angle of the basistipes slightly distal to and beneath the origin of the extensor.

The stipital extensor and flexor of the dististipes of trichopterous larvae are called the levator and depressor of the palp by Das (19). Although they are not inserted on the palp as Das believed, it seems very probable that they are indeed homologous with the levator and depressor of the palp of more primitive insects. That muscles may shift their point of insertion in the course of evolution would appear to be a well established fact; and convincing evidence that this is so is to be found in the muscles of the maxilla, not one of which is inserted at the same point throughout the various orders. So long as there is any doubt as to the homologies of these two muscles they are best referred to as the stipital extensor and the stipital flexor of the dististipes.

Labium

In the Zeugloptera, Trichoptera, Lepidoptera, and Boreidae a large postmentum is present. Muscles neither arise nor are inserted on it except in a few Trichoptera (some Rhyacophilidae and Polycentropidae) in which the

insertions of the tentorial adductors of the basistipes are secondarily displaced on to the mentum. In the Trichoptera the postmentum consists of a distinct mentum and submentum. According to Das (19), the postmental sclerotization sometimes forms a single plate, but I have seen no species in which this occurs. In any event, the mental part may be identified even when entirely membranous because it always bears two innervated setae, although in some (e.g. Hydropsychidae) secondary setae also occur on the mentum as they do in the higher Ditrysia. In the Lepidoptera the postmentum is not as distinctly divided. The mental setae may be absent in some leaf-mining species. The proximal area of the postmentum (submentum) of the Lepidoptera usually has a small but distinct sclerite adjacent to the mesal side of the stipes and cardo. According to Crampton (15, 16), this sclerite is part of the submentum. That this interpretation is correct is to be seen in some larvae, e.g., *Acrobasis* and *Ephestia*, where this sclerite nearly meets its fellow along the median line. These lateral sclerites of the submentum should not be confused with the accessory plate of the cardo, which is present in some larvae. Das (19) considers that these submental sclerites, which he calls basimaxillary sclerites, are neither parts of the postmentum nor the cardo, but it is difficult to see how a sclerite in this region can fail to belong to either the first or second maxilla. In the Zeugloptera the postmentum is not recognizably divided into mentum and submentum, but it has a large membranous anterior part and a heavily sclerotized posterior part. Homologues of the mental setae of the Trichoptera and Lepidoptera are lacking. In the Boreidae the postmentum is only feebly sclerotized. The area of the labium of *Boreus* called the submentum by Potter (50), is, in point of fact, the proximal part of the prementum, as is evident from the insertions of the premental retractors.

In the Mecoptera, Siphonaptera, and Diptera a distinct postmentum is lacking. It may have been gradually reduced until it is now represented by no more than the articulating membrane between the cranium and prementum, or it may have become fused with the cranium. When the function of the labium is considered, the former possibility appears the more likely. The region that Das (19) calls the postmentum in *Bibio* appears to me to be part of the cranium. Cook (12) follows Das in identifying part of the cranium of *Bibio* and other Diptera as the postmentum.

In the Zeugloptera, Trichoptera, and Lepidoptera the oral (dorsal) surface of the prementum probably represents the hypopharynx, and the combined structure may be called the prementó-hypopharyngeal lobe as has been done by Snodgrass. The common duct of the labial (silk) glands opens at the apex of this lobe except in the Lepidoptera in which order the glands open on a projection from the lobe known as the spinneret. A distinct spinneret is present in all free-living lepidopterous larvae but is absent in the sap-feeding early instars—usually only in the first—of some Monotrysia (e.g. *Stigmella*) and Ditrysia (e.g. many Lithocolletidae).

The primitive and maximum number of segments of the labial palpi in the

Panorpoidea is two. In the Trichoptera the labial palpi are one- or two-segmented or may be absent, e.g., some Polycentropidae. They are two-segmented in the Zeugloptera, Boreidae, Mecoptera, and nearly all Lepidoptera. They are one-segmented in the Siphonaptera and one-segmented or absent in the Diptera. Palpal muscles are always absent in larval Panorpoidea, and the absence of palpal muscles probably accounts for Snodgrass's (57) statement that labial palpi are probably absent in caterpillars although these appendages are plainly figured in his diagrams.

A brief summary of the musculature of the labium of larval Panorpoidea is as follows:

Postmental muscles.—Absent except in some Trichoptera in which the tentorial adductors of the stipes are secondarily inserted on the mentum.

Retractors of prementum.—A double muscle in Trichoptera and Lepidoptera inserted on each postero-ventral angle of the prementum. In Trichoptera the smaller of the two arises on the extreme base of the tentorium and the larger beside it on the postoccipital ridge. In Lepidoptera both arise on the transverse tentorial bridge. In both Trichoptera and Lepidoptera these muscles are the retractors of the premento-hypopharyngeal lobe. The origin of the retractors (reductors) of the Zeugloptera could not be determined on my limited material. In Boreidae and Mecoptera the retractors are two muscles arising on the base of the tentorium. In the Siphonaptera the two muscles arise on the postoccipital ridge near the base of the tentorium. In primitive Diptera the retractors are two muscles arising on the cranium or postoccipital ridge, but such muscles are absent in higher Diptera. In *Tipula* but not in other primitive Diptera such as the Bibionidae and Fungivoridae, a large double muscle is inserted on the dorsal part of the heavily sclerotized ring around the orifice of the salivary duct. According to Das (19), this muscle is the median muscle of the prementum. This homology appears to be most unlikely in view of the fact that in no other insect is the median premental retractor inserted on the dorsal side of the common duct of the labial glands. Furthermore, a median premental retractor is absent in Diptera with much less specialized heads, e.g., Bibionidae. This muscle might be thought to be a retractor of the hypopharynx but for the fact that a hypopharyngeal retractor is lost in the whole section of the Panorpoidea to which the Diptera belong. The cranial origin of this muscle makes it unlikely that it is the homologue of the dorsal muscle of the common salivary duct, which arises on the hypopharynx and which is present in some primitive Diptera. For these reasons it seems possible that the double muscle of *Tipula* is a new muscle.

Retractor of hypopharynx.—In Trichoptera and Lepidoptera a pair of muscles inserted on the dorsal arms of the premento-hypopharyngeal lobe are almost certainly the homologues of the retractors of primitive insects. In the Trichoptera these arise on the postoccipital ridge and in the Lepidoptera on the transverse tentorial bridge. In both orders they are the productors of the premento-hypopharyngeal lobe. In the Zeugloptera they apparently

arise on the tentorial bridge. Retractors are absent in the Boreidae, Siphonaptera, and Diptera. They are also absent in *Panorpa*, *Chorista*, *Bittacus*, and probably all Mecoptera.

Palpal muscles.—Absent in all recent orders and therefore probably absent in the common ancestor of the Panorpoidea. Bierbrodt (4) has described palpal muscles in *Panorpa*, but these muscles are inserted on the lobed prementum, each side of which Bierbrodt has mistaken for the first segment of the palp.

Dorsal muscles of common duct of labial glands.—These are probably the homologues of the dorsal muscles of the salivarium of generalised insects. They are present in all Panorpoidea except specialised Diptera. Where a silk-regulator is present, e.g., Zeugloptera, Trichoptera, Lepidoptera, some Fungivoridae, and others, they may be called the dorsal dilators of the silk-regulator.[4] The number of dorsal dilators varies considerably: in Lepidoptera from two to ten pairs and in Trichoptera usually three pairs but five are found in some Hydropsychidae. In the Zeugloptera, Trichoptera, and Lepidoptera the dorsal dilators arise on the dorsal arms of the fused prementum and hypopharynx and are inserted in a dorsal groove of the silk-regulator.

Ventral muscles of the common duct of labial glands.—These are the homologues of the ventral muscles of the salivarium of generalised insects. They are present only in the Zeugloptera, Trichoptera, and Lepidoptera. They function as the ventral dilators of the silk-regulator, but are absent in those Diptera, e.g., some Fungivoridae, that possess a silk-regulator.

Thoracic Legs

The least specialised larval legs of the Panorpoidea are those of the Trichoptera. In only two respects do they differ appreciably from those of insects as primitive as the Thysanura: the tarsus has become one-segmented, and the pretarsus has but a single claw. The trochanter is unusually large and is two-segmented, as it is in some other aquatic larvae, e.g., Odonata and Dytiscidae. The most specialised leg known in the order is the chelate front leg of the rhyacophilid genus *Atropsyche* (41). The fixed finger of the chela is formed by the produced ventral apex of the femur, and the opposed finger by the much shortened tarsus and tibia. Although reduction and even total loss of legs has occurred a number of times in the Lepidoptera, especially amongst leaf-miners, the great majority of caterpillars have legs that are only slightly more specialised than those of the Trichoptera in that the trochanter is very short and more or less fused to the femur. Legs are lost in the

[4] The apparatus that regulates the flow of silk has been called a "silk-press" by Snodgrass (56, 57), Das (19), and others, but the silk is not pressed out, it is pulled out. When the muscles of the silk-regulator contract, they overcome the elasticity of the cuticle, and the duct is opened. The muscles that move the head away from the object on which the silk is stuck provide the force that draws the silk out of the duct, or, when the caterpillar is falling attached to the end of a silk line, gravity is the force that draws out the silk from the duct.

Siphonaptera and Diptera and are much reduced in the Zeugloptera, Boreidae, and Mecoptera.

The musculature of the telopodite of the unspecialised legs of larval Trichoptera and Lepidoptera may be briefly summarised as follows:

Flexor (depressor) of pretarsus.—Numerous fibre bundles arising in both the tibia and femur. In the Lepidoptera one small group of fibres arises on the base of the tarsus.

Flexor (depressor) of tarsus.—A large or small muscle arising in the tibia.

Extensor (levator) of tarsus.—Lost in larval Panorpoidea. This muscle is generally present in the exopterygota, and it is present in adult Panorpoidea, even in such specialized forms as fleas.

Flexor (depressor) of tibia.—One of the largest of the leg muscles. Its fibres arise in the femur except for one group that arises in the trochanter. In the Trichoptera the latter group arises in the distal segment of the trochanter. It has previously been shown (41) that one of the most constant features of the musculature of the legs of both larval and adult apterygote and pterygote insects is that one of the tibial flexors arises in the trochanter.

Extensor (levator) of tibia.—The tibial extensor arises in the femur. It is nearly always a much smaller muscle than its antagonist.

Reductors of femur.—These muscles arise in the trochanter. They are very variable in number, and three (*Hydropsyche*) to six (*Limnephilus*) were present in the Trichoptera examined. One to three femoral reductors were present in all caterpillars seen except *Hepialus*, where reductors are apparently absent.

Flexor of trochanter.—The fibres arise in the coxa, usually near its base, but in the Lepidoptera one group of fibres passes through the coxa and arises in the thorax.

Extensor of trochanter.—In the Trichoptera all fibre groups of this muscle arise in the basal part of the coxa except for one group that extends into the thorax and arises near the median line of the sternum. The latter may be a single large bundle or may be subdivided into a number of smaller bundles. In the Lepidoptera one or more extensor muscles pass through the coxa and arise in the thorax.

It is of some interest to note that reduction has followed quite a different path in the Zeugloptera on the one hand and the Boreidae and Mecoptera on the other. The leg of *Micropteryx* is so reduced that I have been unable to determine the homologies of all of its parts, particularly as I have been unable to distinguish some of its muscles. The leg consists of three segments, including the pretarsus. As in the Lepidoptera, the pretarsal flexor is by far the largest muscle in the telopodite. Since none of the pretarsal flexor fibres arise in the intermediate and longest segment, it seems certain that this segment is the tarsus and not a fused tibio-tarsus because when the tarsus is a distinct segment pretarsal flexors do not arise in it: it is a general rule of arthropod anatomy that the pretarsal flexor fibres do not arise in the tarsus; and the only exception to this rule known to me in the subphylum Antennata

is that one of the smaller groups of flexor fibres of caterpillars arises on the base of the tarsus. The basal segment of the leg clearly consists of the completely fused tibia, femur, and trochanter. The coxa may also be incorporated into this basal segment. A distinct coxa is not present proximally to it. If the suggestion that the coxa is incorporated into the basal segment of the leg be correct, the large muscle that extends through the basal segment into the body is probably the homologue of the trochanterial flexor of the Trichoptera and Lepidoptera that in these two orders extends through the coxa into the thorax.

In the Boreidae (*Boreus*) and in the Mecoptera (*Chorista*, *Panorpa*, *Bittacus*, *Apterobittacus*, *Harpobittacus*) the pretarsus lacks muscles, and no apparent homologue of the pretarsal flexor is present elsewhere in the leg. In the Mecoptera the pretarsus is separated from the segment proximal to it by a poorly defined suture, whereas in *Boreus* the pretarsus is very much more sharply separated from the tarsus. The segment proximal to the tarsus may be the tarsus or the fused tarsus and tibia. If it is the tarsus, the main shaft of the leg consists of the fused tibia, femur, and trochanter. If it is the fused tarsus and tibia, the main shaft of the leg consists only of the femur and trochanter. The insertion of numerous flexors and extensors on the base of the segment immediately proximal to the pretarsus is some evidence that it is the tibio-tarsus, since these flexors and extensors must be the homologues of the tibial flexors and extensors unless we are to believe that all of the telopodite muscles are neoformations. If, as seems most likely, these muscles are indeed the homologues of the tibial flexors and extensors, another interpretation of the leg is possible, namely, that the insertions of the tibial flexors and extensors have become displaced distally and now function as tarsal muscles. In other words, on the latter interpretation the tibia is fused, as in the Zeugloptera, to the femur and not to the tarsus. It may be noted here that in the Hymenoptera (suborder Symphyta) a fusion of tibia and femur has taken place. Yuasa (64) claims that in the Symphyta the tarsus is fused to the pretarsus and the tibia is separate from the femur. However, the origins and insertions of the pretarsal flexor fibres clearly show that he is mistaken. In the Mecoptera and Boreidae the muscles inserted on the base of the femur-tibia are probably the homologues of the trochanterial flexors and extensors, and some of them extend through the coxa into the thorax. The group of fibres inserted on the base of the tarsus that extends through the femur-tibia-trochanter and coxa into the thorax may be a new muscle. In more generalised legs like those of Trichoptera and Lepidoptera there is no muscle that extends from the femur through the trochanter and coxa.

Abdominal Appendages

The Zeugloptera, Trichoptera, Lepidoptera, Boreidae, Mecoptera, Siphonaptera, and some Diptera (e.g. Tendipedidae) have ten discrete abdominal segments. Most Diptera have only eight discrete abdominal segments, and the postabdominal spiracles are terminal or nearly so. The

structure and distribution of the prolegs has recently been described in some detail (43). It has been shown that the prolegs of segments other than the tenth are secondary adaptive structures not serially homologous with the thoracic legs. In each order they have arisen independently, and within the Diptera they have been independently evolved at least 27 times. Ventral prolegs are absent in the Trichoptera, Boreidae, and Siphonaptera, lack muscles in the Zeugloptera and Mecoptera, and have retractor muscles in the Lepidoptera and Diptera. The prolegs of the tenth segment of the Lepidoptera, Siphonaptera, and Diptera are secondary adaptive structures, but there is little evidence for or against the view that anal prolegs of the Trichoptera are homologous with anal cerci. But, whether they are neoformations or modified anal cerci, the more complex their structure and the more they come to resemble thoracic legs, the more they have departed from their ancestral form (43).

Tracheal System

The primitive number of tracheo-spiracular metameres in pterygote insects is 10, and 10 are present in all panorpoid larvae. It has been claimed (45) that in some Tendipedidae the tracheal system does not develop until the late larval stages, and these may therefore constitute an exception amongst panorpoid larvae. In all panorpoid larvae the first pair of spiracles, the mesothoracic, always migrates on to the prothorax during embryogenesis. All larval stages of the Trichoptera are apneustic, and the tracheal system remains apneustic in larvae (*Enoicyla*, Limnephilidae) that have become secondarily terrestrial. In the Zeugloptera the tracheal system appears to be holopneustic: the two pairs of thoracic spiracles are functional as are the first seven abdominal. I have been unable to detect either functional or nonfunctional spiracles on the eighth abdominal segment, although I have injected seven larvae with cobalt sulphide. Tillyard (61) claims that *Sabatinca* is peripneustic, but I am not convinced that he has seen its spiracles. In terrestrial Lepidoptera, Boreidae, and Mecoptera the tracheal system is always peripneustic, the metathoracic spiracles always being nonfunctional. In aquatic Pyralidae all larval stages may be apneustic (*Acentropus*), or the early stages may be apneustic and the last peripneustic (some *Nymphula*) or with functional spiracles only on the first three abdominal segments (other *Nymphula*). The Siphonaptera are peripneustic in the first two instars and holopneustic in the third (54). The first instar larva of the Diptera is apneustic or metapneustic.[5] Later instars may be apneustic, metapneustic, propneustic, amphipneustic, hemipneustic (only Fungivoridae), or holopneustic (only Bibionidae), and whenever there is a difference in the number of functional spiracles in two instars, the number of functional spiracles of the earlier instar is less than that of the later instar (37).

[5] In a few Muscidae, e.g., *Limnophora riparia* (Fallén), the newly hatched larva appears to be in its third instar (46). Such species are amphipneustic on emergence from the egg.

The moulting process of nonfunctional spiracles is always of the primitive type. When the spiracle has cuticular structures that would prevent the withdrawal of the old trachea through it, the moulting process is either of the *panorpoid* or *elateroid* type (37). The moulting process of the functional spiracles of the Zeugloptera, Lepidoptera, and Siphonaptera is of the primitive type. The Mecoptera have the panorpoid process. Amongst the Diptera the process may be primitive (Culicidae), panorpoid (e.g. Bibionidae, Trichoceridae, Tipulidae), or elateroid (Anisopodidae, Fungivoridae, most (all?) Cyclorrhapha). The moulting process of the Boreidae is not known to me, but it is either panorpoid or elateroid.

Amongst insects a spiracular regulatory apparatus provided with muscles is primitively lacking only in the Thysanura. The functional spiracles of the Zeugloptera, Lepidoptera, Boreidae, Mecoptera, and Siphonaptera have a regulatory apparatus at the junction of the trachea and the spiracular atrium. The common ancestor of recent Diptera had secondarily lost the regulatory apparatus, and in conformity with Dollo's generalization no recent dipterous larvae have re-evolved such an apparatus (42).[6] The closing apparatus of the postabdominal spiracles of the Stratiomyidae is external to the spiracles: in amphipneustic stages the anterior thoracic spiracles lack a closing apparatus (42). In dipterous larvae that are normally exposed to relatively dry environments, loss of water through the spiracles is often reduced by the "felting" in the spiracular atrium, which serves to establish a humidity gradient.

THE COMMON ANCESTOR OF RECENT PANORPOIDEA

The review of the anatomy of the larvae of recent panorpoid orders given in the preceding pages makes it possible to describe in considerable detail and with considerable confidence the structure of the larva of the common ancestor of these orders. The following summary of the structure of the common ancestor necessarily assumes the irreversibility of evolution with respect to complex structures. For instance, in some recent orders the trochanter is completely fused to the segment before or behind, whereas in others it is separate: it is assumed that a larva with a fused trochanter can be derived from an ancestor with a separate trochanter but one with a separate trochanter cannot be derived from an ancestor with a fused trochanter.

Cranium with a ⅄-shaped cleavage line, the arms of which extend through the cranial areas that intervene between the origins of the mandibular muscles and those of the facial muscles. Epistomal suture probably present. Tentorium with anterior and posterior arms; posterior pits on postoccipital ridge; tentorial bridge present. *Labrum* with lateral retractor muscles inserted on tormae; with median retractors and with compressor muscles. *Compound eyes* present; lateral ocelli absent. *Antenna* with retractor muscles

[6] Séguy (53) claims that the spiracles have a closing apparatus!

arising on anterior arm of tentorium; without intrinsic muscles in first segment. *Maxilla* with cardo not fused to stipes; cranial promotors of cardo absent but tentorial adductors present. Stipes subdivided into a basi- and a dististipes; basistipes with tentorial adductors, and dististipes with both cranial flexors and extensors as well as stipital flexors and extensors. Maxillary palp without muscles. Galea and lacinia not fused and without flexors. *Labium* with postmentum probably subdivided; postmental muscles absent. Prementum with palp 2-segmented, without palpal muscles; premental retractor present and arising near base of posterior tentorial arm or on postoccipital ridge beside it. Hypopharyngeal retractors present, probably arising on tentorial bridge. Labial glands with both dorsal and ventral dilator muscles of common duct. *Legs* six-segmented (coxa, trochanter, femur, tibia, tarsus, pretarsus), with tarsus undivided and pretarsus with a single claw. Pretarsal flexor arising in both tibia and femur, extensor absent. Tarsus with flexor arising in tibia, extensor absent. Tibia with most of flexor fibres arising in femur but one group arising in trochanter; extensor arising in femur. Femur with reductors arising in trochanter, probably two groups of fibres. Trochanter with flexor arising in coxa; most extensor fibres arising in coxa but with at least one group of fibres arising in thorax. *Abdomen* without ventral prolegs. *Tracheal system* holopneustic in later instars; probably holopneustic in first but, if not, peripneustic. Moulting process of all spiracles of the primitive type. Spiracular regulatory apparatus present at junction of trachea and spiracular atrium.

This description of the larva of the common ancestor of recent panorpoid orders shows at once that this insect cannot be placed in the order Mecoptera. It possesses the sum total of the primitive features distributed amongst all recent Panorpoidea. It differs in the following important particulars from the Mecoptera: (*a*) the labrum has lateral retractor muscles; (*b*) the antennal retractors arise on the tentorium instead of the cranium; (*c*) the cardo is not fused to the basistipes; (*d*) the galea and lacinia are not fused; (*e*) a well developed postmentum is present; (*f*) the hypopharynx has retractor muscles; (*g*) the common duct of the labial glands has ventral dilator muscles; (*h*) the legs are six-segmented with a separate trochanter and a pretarsal flexor inserted in the pretarsus instead of being much reduced, without a separate trochanter, and without a muscle inserted in the pretarsus; (*i*) the tracheal system is holopneustic instead of peripneustic; and (*j*) the moulting process of the spiracles is of the primitive type instead of the panorpoid type.

If a group of fossil animals is known to have given rise to the recent orders A, B, and C, to place the group in the recent order A is to create a polyphyletic order in terms of B and C. If it be placed in B, then B is polyphyletic in terms of A and C, and so on. A taxonomic group (genus, family, order, etc.) can only be polyphyletic in terms of another group, never in terms of itself. At any taxonomic level, the preferred nomenclature is that which most nearly reflects the relative times of divergence of the different groups. Polyphyletic

categories are inevitably created when relative times of divergence are reversed.[7] To place the Permian Orthophlebiidae (or related families) in the order Mecoptera with recent Mecoptera is to create a polyphyletic order in terms of other panorpoid orders. To place the Orthophlebiidae in the Mecoptera is to say that they are more nearly related to the Mecoptera than to other panorpoid orders, that they are more nearly related to the Mecoptera than are the Siphonaptera and Diptera to the Mecoptera, which is absurd.

How has it happened that Tillyard, Martynov, Carpenter, and others have without question placed Permian and later ancestors of *all* recent panorpoid orders together with recent Mecoptera in the one order? This could only have occurred by ignoring the basic principles of phylogeny. A contributory cause was perhaps the fact that hardly anything is known of the structure of the Orthophlebiidae [*sensu* Carpenter (6)] and related families. Practically all of the work on these fossils is based on one character, wing venation. It is worth noting in this connection that, by the method of these writers, if only larval legs were preserved, the Orthophlebiidae and their relatives would be placed in the Trichoptera, if only larval maxillae were preserved as fossils in the Zeuglotpera, and so on. In short, phylogenists must not overlook one of the most general laws of evolution, which is the law of unequal development: not only do different groups evolve at different rates, but within any group the organ systems themselves evolve at different rates.[8] This is why most animals are such mixtures of specialised and primitive features. For instance, as is recognized by Imms (44) and others, the Mecoptera are very closely related to the Diptera, the most highly specialised of the panorpoid orders, but in respect of two characters they are more primitive than any recent order: the possession of compound eyes in the larval stage and the character of their wing venation.

THE ORDER ZEUGLOPTERA

Chapman (7) erected the order Zeugloptera to contain the family Micropterygidae. Tillyard (60, 61, 62) again included the family in the Lepidoptera. The group was once more elevated to ordinal rank by Hinton (35), but not for the reasons given by Chapman. A few years later Dumbleton (20) criticised the views expressed by me and once more reduced the Micropterygidae to family rank within the Lepidoptera on the basis of the structure of the genus *Agathiphaga*. Dumbleton kindly sent me a larva of *Agathiphaga*. This genus belongs to the Eriocraniidae or a closely related family: it is a typical lepidopterous larva with none of the distinguishing features of the Micropterygidae. Dumbleton's criticisms are therefore without foundation.

I am aware of no reason for excluding the Micropterygidae from the

[7] These principles of classification are briefly discussed by Hinton (39, pp. 22–23) and in much detail by Hennig (32, 33). Somewhat similar views were earlier expressed by Säve-Söderberg (52).

[8] This law was well known to many 19th century writers. It has recently been called "Watson's Rule" by de Beer (3).

Lepidoptera on the basis of adult structure: with the discovery of the genus *Agathiphaga* by Dumbleton, the suborder Dacnonypha now contains species with functional mandibles and a nonspecialised galea. The pupa likewise provides no reason for their exclusion from the Lepidoptera. The pupa is decticous (36, 40), as is the pupa of the suborder Dacnonypha. There exist, however, many important differences between the larvae of the Zeugloptera and Lepidoptera: (*a*) the cranium of the Zeugloptera lacks the adfrontal ridge and adfrontal sutures; (*b*) the tentorial bridge is short and broad as in the Mecoptera instead of being long and narrow; (*c*) the anterior tentorial pit is close to the inner side of the antennal base instead of far behind the antenna; (*d*) the maxilla has a separate galea and lacinia instead of an undivided lobe; (*e*) a cranial flexor of the dististipes is present; (*f*) lateral labral retractors are present; (*g*) a pair of cibarial muscles is inserted in the labrum; (*h*) a spinneret is absent; (*i*) the leg has the coxa, trochanter, and femur fused but the tarsus and pretarsus are discrete segments, a type of reduction unknown in the Lepidoptera; (*j*) the ventral abdominal prolegs lack retractor muscles; (*k*) the spiracles of the metathorax are functional instead of nonfunctional; and (*l*) the chaetotaxy of the thorax and abdomen is of quite a different type: the distribution of the primary setae of the two orders is entirely different.

In many respects, especially in the structure and musculature of the head and mouth-parts of the larva, the Zeugloptera appear to be much more closely related to the Trichoptera than to the Lepidoptera. The panorpoid orders form two natural sections, the Zeugloptera-Trichoptera-Lepidoptera and the Siphonaptera-Mecoptera-Diptera, with the Boreidae in many respects intermediate between them. The female is the heterogametic sex in the Trichoptera and Lepidoptera, but it is not known which is the heterogametic sex in the Zeugloptera. In the Boreidae (14) and other panorpoid orders the male is the heterogametic sex. From a phylogenetic point of view there seems to be little choice between treating the Zeugloptera, Trichoptera, and Lepidoptera as distinct orders or as distinct suborders within one order.

ORDER NEOMECOPTERA, NEW STATUS

Crampton (17) erected the suborder Neomecoptera to contain the family Boreidae, and this suborder is here elevated to ordinal rank. The chief distinctions between the Neomecoptera and Mecoptera may be briefly summarised. *Larva:* (*a*) the cranium is without a distinct epistomal suture; (*b*) the cardo is not fused to the basistipes, and the tentorial adductors of the cardo are present; if homologues of these muscles are present in the Mecoptera they are now tentorial adductors of the cardostipes; (*c*) the postmentum is well developed instead of lost or reduced to an articulating membrane between the prementum and the cranium; (*d*) the abdomen lacks prolegs, whereas in the Mecoptera prolegs are present on the first eight abdominal segments; and (*e*) the larvae feed on moss, whereas those of the Mecoptera are carnivorous. *Adult:* (*a*) the ovaries are panoistic (13, 59) instead of poly-

trophic as in the Mecoptera (31); (*b*) the 11th abdominal segment of the female lacks cerci, whereas one- or two-segmented cerci are present in the Mecoptera; (*c*) the ninth and tenth abdominal segments are modified to form a large functional ovipositor but no such "ovipositor" is found in the Mecoptera; and (*d*) the adult gut lacks the six especial rectal glands of the Mecoptera (51).

Many other differences between *Boreus* and the Mecoptera could be cited from the literature, but their significance is not clear. For instance, a number of differences between the adult thoracic muscles of *Boreus* and *Panorpa* are given by Füller (30), but it is necessary to know the thoracic musculature of wingless Mecoptera in more detail before the phylogenetic significance, if any, of such differences can be determined.

The pupa of *Boreus* is decticous like that of the Mecoptera, Zeugloptera, Trichoptera, and Dacnonypha (36, 40). The decticous pupae of these orders are all much alike and do not provide any specifically pupal characters of value in assessing ordinal inter-relations.

Attempts to derive fleas from dipterous-like ancestors have often been made. On the basis of adult structure Crampton (18) and Tillyard (63) have shown that such a derivation cannot be accepted. It may here be noted that the peripneustic respiratory system of the first instar larva of fleas also forbids such a derivation. From this it follows that the adecticous-obtect pupae of fleas and Diptera have been evolved independently from a decticous pupa. On the basis of larval structure, fleas could be derived from a *Boreus*-like ancestor with simple annular spiracles. In this connection it is worth noting the claim (which I have not verified) that among the Panorpoidea only the Siphonaptera and Boreidae have panoistic ovaries.

The orders, suborders, and other higher categories of the Panorpoidea discussed in this paper are listed here for the convenience and orientation of the reader:

Superorder PANORPOIDEA

Order ZEUGLOPTERA Chapman, 1917
  Micropterygidae only
Order TRICHOPTERA Kirby, 1813
Order LEPIDOPTERA Linnaeus, 1758
  DACNONYPHA Hinton, 1946
    Eriocraniidae and a few others
  MONTRYSIA Börner, 1925
    Hepialidae, Stigmellidae, Adelidae and a few others
  DITRYSIA Börner, 1925
    Most Lepidoptera
Order NEOMECOPTERA Crampton, 1930, *new status*
  Boreidae only
Order SIPHONAPTERA Latreille, 1798
Order MECOPTERA Comstock, 1895

Order DIPTERA Linnaeus, 1758
NEMATOCERA Latreille, 1825
BRACHYCHERA Macquart, 1834
ORTHORRHAPHA Brauer, 1863
CYCLORRHAPHA Brauer, 1863

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ZOOGEOGRAPHY OF INSECTS[1]

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The study of the geographical distribution of insects is a subject which has received attention from many entomologists, yet one which is still in an infant stage of development. Knowledge of the distribution of higher vertebrates has progressed to the point where it is fairly well understood, but this is by no means true for insects. Not only are very many insects yet to be discovered or named, but the complete distribution is known for very few. Also, rather little is known of the evolutionary history of insects and there is much contradiction among conclusions relating to the history of insect distribution.

It is important enough to know the ranges of the species that occur in an area, in searching for biological control agents, in evaluating pest potentials, crop selection and danger from diseases of plants, animals and man; but zoogeography is much more, however, than the mere determination of the ranges of species or groups. It is, furthermore, a field of interrelation of ecology, physiology, systematics, phylogeny, paleontology, geography and geology. It is not a static subject but dynamically relates the tolerances of individuals and populations to their origin, evolution, and dispersal in terms of changing climates, vegetation and topography.

The study of insect distribution has progressed to very different degrees in different parts of the world, and for different groups of insects, more or less in proportion to the extent of entomological research. In Europe, where the species and their respective ranges are well known in most groups, very thorough studies have been possible. In some cases it has apparently been possible to work out in detail not only present but past distribution. In other continents where species are still being described and their ranges determined, much pioneering work remains to be done. In few groups of insects has it been possible to determine the course of development and spread of the world fauna, but in recent years a few excellent attempts have been made (168, 121).

Though the extremes of geographical range of a species may be easily outlined on a map, it must be remembered that the actual occurrence of a species in most cases involves not only discontinuous macrogeographic distribution, but also limitation to a specialized niche within the areal range. Distribution maps should show occurrence by dots, and be supplemented by indication of niche and general habitat or zone, in addition to recording of place-names. More emphasis is now being given to the importance of ecology in zoogeography.

The application of insect zoogeography to phylogeny and systematics is

[1] The survey of the literature pertaining to this review was completed in June, 1957. The author has not seen proofs.

treated in great detail by Hennig (80), who stresses ecology and chorology, cites former glacial refuges as centers of multiplication, and states that the named synonyms of widespread species are often described from the margins of their ranges.

Methods

Ross (168) has presented a plan of procedure for interpreting the evolution and distribution of a group, based on his work with caddisflies. First, one must study the characters of living and fossil species and work out phylogeny and distribution patterns. These patterns should then be correlated with the geological time scale using the dated fossils. The geological data then show dispersal possibilities, and comparisons may be made with known history of other groups. The more definite and complete the data, of course, the more reliable are the conclusions. Naturally larger groups including fossil material offer greater possibilities of solution. In determining routes of dispersal, qualitative approach is essential, rather than statistical, as shown by Kinsey (99) for an annectant series with the most primitive in southern Mexico, which was determined as the original home. In integrating phylogeny and distribution, changes in environment, extinction of lines, and variation in both rate of evolution and rate of dispersal must be borne in mind. And with isolated species, or sister groups on separate continents, the point of origin may be indeterminable without other evidence.

Dispersal

That the living species of insects have not evolved continuously in the same areas they now inhabit is generally accepted. It is also well established that there have been climatic changes or cyles. In the Pleistocene Period there were four ice ages associated with some shifting of the poles of the earth, extension of ice caps southward in Europe and North America, and lowering of the sea level. Farther back, the climates are less well known, but fossils of tropical animals and plants have been found in rocks of various periods in areas of cool climate today. There is some evidence to indicate that insects do not quickly change their climatic tolerances. One line of evidence is the occurrence together in ancient deposits of fossils of various groups which have similar macroclimatic tolerances today. Other evidence includes some parallels between the evolution and dispersal of insects and host-plants to which they are attached [Gressitt (69)], or correlation with other niches [Ross (168)]. Studies of both cold-adapted and warm-adapted groups [Emerson (48)] indicate somewhat similar dispersals at different times. In New Guinea there has been some radiating of tropical forms into high young mountains which lacked a temperate fauna (73, 189).

This field has been treated recently by Williams (204). The power of dispersal,[2] or vagility, seems to be characteristic of living things, but various

[2] The term "migration" should be reserved for movement of insects in a direction or for a distance over which they have control.

groups spread in differing ways, and at varying rates. So many factors are involved in rate of dispersal, that it can probably never be determined to the satisfaction of all, particularly for past ancestors. Normal population pressure and the consequent tendency to spread is tempered by competition within the species and with other forms and numerous climatic and other factors. Andrewartha & Birch (2) stress the innate tendency toward dispersal among insects, and state that accentuation of dispersal tendencies as a result of overcrowding of populations may or may not result in extension of range.

In addition to normal vagility, passive (accidental) dispersal must often enter in. This may consist of transport in air currents, on the bodies of birds or other animals, on streams, floating logs, or by other accidents (10, 34, 46, 65, 66, 70, 72, 74, 209). Air currents seem to play a most important role, and various evidence seems to point particularly to this factor in the dispersal of insects to oceanic islands. Wellington (202) has discussed the physical factors involved in air dispersal of insects, indicating that long-distance dispersal is negligible, and short-distance dispersal is common, from the standpoint of dispersal of pests in continental areas. Gislen (65) considers that minute insects are so easily carried by air that they are not subject to the same distributional limitations as other insects and are therefore of no significance in zoogeography. Salmon (171) and Mockford & Gurney (137) would appear to dispute this to some degree, from the data they present on faunal differences for some small insects. Gislen states that the greatest limiting factor in air transport is desiccation, which is serious only in clear weather; but he may minimize the adverse factors. Palmén (147) describes great numbers of insects washed up on beaches in Finland, many of them alive, and mostly winged insects. Heberdey (79), in discussing range extension, stresses the importance of means of dispersal in determining phylogenetic age on a distributional basis. Savile (173) treats dispersal rates.

In estimating the degree of relationship of different zoogeographical regions, attention must be paid to the movements of man as well as other natural factors, particularly for the noneconomic species. The spread of pests is often clearly traceable, but not so with noneconomic species which may have been transported to new areas where thorough collecting has rarely been done in advance. Lindroth (117) demonstrates in detail that many species of ground-inhabiting beetles, and other insects, were transported from southwestern England to Newfoundland and to the Maritime Provinces of Canada in rock and soil ballast on ships going for lumber in early colonial days. Since the climates of the two areas are similar, many colonizations succeeded, and there are about ten times as many insects introduced from Europe to North America as the reverse. Palmén (148) shows that of 42 species of myriapods and terrestrial isopods in Newfoundland, 36 are European, two cosmopolitan, and only five American. Gurney (74) treats this question for some of the lower orders of insects.

Lindroth (115) believes that attempts to correlate the ranges of insects with isotherms or other climatic averages is an incorrect practice, for micro-

climatological differences are very great, and control actual distribution in the main. Though many workers have placed temperature as the most important factor controlling insect occurrence, other factors, particularly humidity, may be most the important. Lindroth (115) has shown that some apparent association of ground beetles with limestone actually proved to be controlled by thermal and hygric, rather than chemical, factors. In response to this, Janssens (91) insists that there are definite associations of insects with limestone. The most thorough treatment of the operation of factors affecting insect distribution is that of Andrewartha & Birch (2). Some important aspects of the relation of climatic factors to distribution were introduced by Matthew (128). The effects that changes in the environment have on distribution is treated by Franz (59), who shows that the more frequent the changes, the poorer the fauna. Cold relicts are frequently found among insects, but not so with warm-blooded animals, and warm relicts are rarely found among insects [Lindroth (115)]. Races may be produced more rapidly on small islands, isolated peaks or valleys, and during periods of changing climate.

The work of Schilder (174) emphasizes the importance of isolation in the development of races, but neglects aspects of historical geology and uses some examples based on outdated taxonomy. Iablokoff (88) discusses biotic factors and an ecological plasticity in relation to distribution.

Ross & King (170) develop the hypothesis that a species becomes adapted to a particular ecological niche and stays there as long as it survives. If the species, or part of it, is able to move into a different ecological niche, selection pressures of the new environment will favor beneficial genetic changes in the population. If then, through geographic isolation, many species arise from a single one, the least changed or primitive species should represent the one still remaining in the ancestral habitat, and the most changed or specialized species should be the one in the habitat differing most from the ancestral habitat.

Although the knowledge of insect zoogeography is imperfect and uneven, some firm bases have been laid for zoogeography in general, especially for the higher vertebrate animals (82, 131, 132, 133, 143, 181). Only minor changes have been made in the outlines of Wallace's zoogeographical regions (200), and there still remain disagreements on some of these changes. The recent, excellent general treatment of zoogeography by Darlington (38) largely concerns the better known vertebrates.

The importance of ecology to distribution is stressed by Janssens (91, 92), who indicates that phytogeography has progressed beyond zoogeography, and makes some vigorous criticism of much of the work concerning insect distribution. Kiriakoff (100, 101) praises Janssens' papers but states that to accept them fully endangers phylogeny, but agrees on the importance of ecology. Kiriakoff thinks that in many of the cases where genera are reported as found in different southern continents, actually different genera are involved, indicating older separation. Hennig (80) & Brehm (16) relate distribution and taxonomic characters.

Zoogeographical Regions

Wallace (200) established six zoogeographical regions: Palearctic, Ethiopian, Oriental, Australian, Nearctic and Neotropical. These are not of equal distinction, and may be arranged in groups. Palearctic and Nearctic, the north temperate regions, are very closely related, and are often treated as subgroups of the Holarctic Region. Though there is invasion of the Nearctic from the Neotropical, and Palearctic from Oriental, the Palearctic and Nearctic have more in common, showing that climate and history are more important than present geographical continguity. The Ethiopian is most clearly related to the Oriental Region, though the former has some exchange with the Mediterranean Subregion of the Palearctic. Ethiopian and Oriental are sometimes combined as Paleotropical, which to some also includes the Australian Region. Nearctic, Palearctic, Ethiopian and Oriental are sometimes grouped together as Arctogaea, while Neotropical is segregated as Neogaea and Australian as Notogaea. Two large islands with associated smaller islands having distinctive faunae, Madagascar and New Guinea, do not fit perfectly into the above systems. Another classification of regions is by type of barriers [Darlington (36, 38)]; the climate-limited regions being the Palearctic and Nearctic, the barrier-limited regions being the Neotropical, Australian and Malagasy, and the main regions (which are in part barrier- and climate-limited) being Ethiopian and Oriental.

To some workers, the zoogeographical regions are purely arbitrary divisions, and some feel that the drawing of outlines of common or average ranges of groups of species has no real significance because factors controlling distribution of different groups may be quite unrelated.

The desert areas of North Africa and Southwest Asia form a unit as important as a zoogeographical region according to Uvarov (192), although they cannot be outlined satisfactorily on a map. Uvarov uses the term ecofauna to designate the lowest zoogeographical units. For the Sahara (193) he designates four ecofaunae: deserticolous, saxicolous (on rocky country), arbusticolous (among trees) and graminicolous (among grasses). Most species would be involved in only one of these ecofaunae, but each ecofauna may include forms of various origins, such as Paneremian (widespread desert forms), Ethiopian, Lemurian, and Angaran.

In spite of the fact that South America, Africa and Australia are each separated in one of the three major divisions of the world, the southern portions of each have numerous elements in common in many groups of insects [Edmunds (44); Hardy (77)], vertebrates and plants. The fossil evidence for insects is imperfect, but in plants a conspicuous ancient southern group, typified by *Glossopteris*, is characteristic of these areas and of Antarctica (Seymour Island, 64°S., south of the northern tip of the continent). This and other evidence has been the basis for the Wegenerian Hypothesis, or theory of continental drift, which explains the origin of continents as starting with a single southern continent. This continent cracked into the forms of the present continents and drifted apart and northwards to their present positions. This theory is firmly adhered to by many European workers

[Demoulin (41); Fraser (60); Maran (125)], and one of its stoutest champions is Jeannel (93, 94). Fraser cites yearly westward flights of butterflies and dragonflies from the Western Ghats in India to the Indian Ocean as evidence of continental drift. Mammalogists, who have abundant fossil evidence [Simpson (181)], can show that changing climates, and a Bering Straits connection between Asia and North America (also abundantly shown by fossil florae) and old connections between Asia and Australia, can account for present distribution in the main. Rehn (157) and others point out that continental drift creates many new problems. Rehn also severely criticizes Jeannel's attributing similarity of Nearctic and Palearctic faunae to a Greenland-Iceland-Europe connection (93), because there is little actual evidence for that, but much for the Siberia-Alaska connection. Detailed treatment of the Pleistocene ice ages is given by Flint (56).

Another argument against the Wegenerian Hypothesis is the weight of evidence for the permanence of the present oceans. Wallace (200) dwelt on this, as have many since then. Although there is evidence of more extensive former islands in the mid-Pacific [Hamilton (76)], these were still surrounded by deep ocean. They could have served as stepping stones in the dispersal of insects to the more isolated island groups, like Hawaii. Likewise, there is little likelihood that the mid-Atlantic ridge once formed a continent "Atlantis," as described by Malaise (122) and others.

Many workers, in order to explain apparent close relationships of insects on distant continents or islands, have hypothecated land bridges permitting dispersal from one area to another. In most cases these enthusiasts have failed to explain the lack of other dispersals which such bridges might have permitted. The evidence for air transport of insects can in most cases reasonably explain the populating of oceanic islands, and the evidence for changing climates and the Bering land bridge can explain most continental relationships, through long-distance dispersal.

Munroe (141) demonstrates methods of comparing related faunae, showing that comparison of vicarious elements of shared superspecies provided a good measure of differences between faunae in which autochthonous radiative evolution is not an important factor, but the historical interpretation is difficult.

Ross (168) demonstrates for certain Trichoptera that during the Cretaceous there was wide dispersal of primitive forms; in the Paleocene the greatest dispersal of cold-adapted types, in the Eocene the greatest dispersal of subtropical forms, during the mid-Cenozoic the greatest dispersal of temperate forms, and in the Pliocene and Pleistocene chiefly intrasystem dispersal of montane elements. Ross states that these groups show that dispersal to the southern continents had their origins in the northern hemisphere, and that Africa, particularly, had infrequent cool climate connections with the north. Seevers (177) admirably delineates spread and evolution of termitophilous Staphylinidae in relation to the same for termites, correlating his findings with those of Emerson (48).

Holarctic.—Most of the recent workers (38, 48, 116, 168, 181) ascribe all interchange between Eurasia and North America requiring continuous land connection to have taken place across the Bering bridge at various periods. Ross (168) cites seven possible Cenozoic connections: Paleocene, early Eocene, late Eocene to early Oligocene, early to mid-Miocene, late Miocene, late Pliocene, and Pleistocene, with the most extensive exchange in the early Eocene and Pleistocene connections. Though Emerson (48) felt that late Cretaceous was the last time tropical forms could cross the bridge, Ross thinks it may have been later. Lindroth (116, 117) treats in detail the relationships of the Palearctic and Nearctic. Obenberger (144) discusses the relationship in the Buprestidae. The north-south nature of the North American mountains, and the more east-west alignment of the Eurasian ranges provided different situations, particularly as regards southward migration during glaciation. Gurney (74) has also discussed species in common between the Nearctic and Palearctic.

Palearctic.—The Palearctic insect fauna is rich and varied, but lacks many Ethiopian and Oriental types barred by climatic factors. The fauna is probably more varied at the east and west extremes—in Japan, Northeast Asia, and Europe—than in the intermediate area between which is more strictly bounded on the south by both deserts and very high mountains. In the east and west extremes, the environments are more varied, and mixtures from the neighboring regions have occurred. Many species in Europe and Japan are closely related or identical. The Mediterranean Subregion is fairly arid and poorer in representation of many groups than both Central Europe and the Ethiopian Region. The Manchurian, or Japanese Subregion is extremely rich and varied, having some elements otherwise known only from Western, or Eastern, North America, and many others which have extended northward from the Oriental Region, with the lack of effective barrier between, and the coastal areas washed by the warm sea current. Warnecke (201) discusses the northern Palearctic fauna, stressing Angara origin. In Europe there is considerable north-south discontinuous distribution, frequently involving Fennoscandia in the north and the Alps, Pyrenees, Caucasus and other mountains in the south. Much of this is result of the advance and retreat of the glacial period ice sheet, pushing populations southward and leaving many in isolated pockets in the southern mountains as glacial relicts. Studies of relicts in particular groups are treated by Daniel (33), Reiss (159), and others. There exist in Europe many remarkable specialized and localized cave-inhabiting insects of many groups. The distribution of these has been treated by Holdhaus (84) and Jeannel (93). The European fresh water fauna is treated in detail by Theinemann (188), particularly from the standpoint of glacial influence. For the European boreo-alpine Orthoptera, Anders (1) points out that many of the north-south isolations are independent, and developed at different times, and that many of them represented Angara elements which came in from Siberia because they were already cold-resistant at start of the fourth ice age. Jordan (96) treats ice relicts on cold

moors, and states that *Notonecta lutea* is frozen 260 days of the year. The taiga (coniferous forest) fauna is treated by Florov (57).

The fauna of the British Isles is one of the very best known. According to Beirne (7), it includes over 20,000 species of insects, one-half the fauna of Europe. There are three centers of distribution: south and southeast, highlands of Scotland, and the southwest. About one-half the species occur in Ireland, but there are few endemics there. Of the total, 2 per cent or less are endemic, although there are many endemic subspecies. There has been much exhange back and forth with the continent. Berine states that 35 per cent could have been carried by air, but probably 95 per cent spread over land connections as the fauna is quite harmonic. There have been several connections during the past 600,000 years. Even skeletons of large land animals have been found on Doggersland, a sunken connection lying west of Netherlands. If it is true that the temperate (less cold-adapted) insects in England are post-glacial invaders, then evolution (with small populations) has been rapid and many new species have evolved in the past 6,000 years. But other evidence indicates that it took over 100,000 years to produce many of the endemic subspecies. Kruseman (103) discusses a *Bombus* which may be a relict of Doggersland, pointing out that some species have one subspecies on both sides of the English Channel and another subspecies in eastern Holland and Germany. Very detailed studies have been made for various parts of Europe (31, 115 and others).

Baltic aquatic glacial relicts are discussed by Lindberg (113) showing that the weakly saline nature of the Baltic Sea renders rather slight the distinction between fresh-water and sea habitat, with many insects in the shore water. In general, the fresh-water rock pools contain insects of the far north, and the brackish pools harbor more southern insects at the north ends of their ranges. Szent-Ivany (186) shows western Hungary to be a faunal meeting place, with alpine and Mediterranean elements more numerous than the Ponto-pannonic and Carpathian elements. For the Middle East, Theodor (187) shows that the Diptera fauna is mainly Palearctic with northern species spreading southward to varying degrees and Mediterranean species spreading eastward, in many cases into northwest India.

The Atlantic islands are volcanic and populated by air and sea currents, according to Balachowsky (3) and others. According to Lindberg (114) the Canaries and Cape Verde Islands were never connected, but both have been joined to Africa. The younger steppe fauna consists of small winged insects which came through wind dispersal; the older fauna is limited, and in the mountains. Chopard (30) shows that the Azores and Madeira have an impoverished Mediterranean fauna, the Canaries a richer, more distinctive Mediterranean fauna with some African elements, and the Cape Verdes an Ethiopian fauna with feeble endemism.

Nearctic.—In discussing the origin of the Nearctic insect fauna, Ross (167) indicates general dispersal in Cretaceous and later with many colonizations from Asia and South America. There was relatively little extermina-

tion during glacial periods, and much multiplication of species and southward spread. There is also no evidence of connections between the mountains of eastern and western North America. In treating the origin of the northern Nearctic fauna, Munroe (142) shows that most of Canada was glaciated in the Wisconsin Period, but that there were Amphiberingian refuges, as well as other refuges on the coasts, and perhaps in Greenland. There are ten types of existing distributions: circumpolar, widely distributed American, Amphiberingian, Alaskan, Pacific-coastal, Cordilleran, Amphi-Atlantic, high Arctic American, northwest Canadian and northeast Canadian.

For Greenland, Strenzke *et al.* (185) show that of the soil fauna, 23 species are of wide Arctic to subtropical distribution, 13 are Arctic or upper Palearctic, and four are endemic but may be found later elsewhere. Vibe (97) stresses the circumpolar elements. Within Greenland, de Lesse (111) shows that distribution zones are determined largely by amount of sunshine. The life zones in Alaska, according to Mason (127), are Canadian, Hudsonian and Arctic, with five main distribution patterns. Klots (102) shows that many species have their southernmost extensions in Appalachian acid bogs, as well as Alpine areas. Darlington (34) shows how the insect fauna of the Antilles could largely have come by air dispersal. Dillon (43) has discussed in detail the climate of the Wisconsin Period (last glacial) in North America, in relation to insect distribution. Van Dyke (194) discussed the North American beetle fauna, showing eight distinct faunae, of which five are derived from Eurasia across the Bering bridge, and three derived from South America, none being of North American origin. He stresses the diversity and distinctiveness of the Vancouveran fauna, which nevertheless is derived from northeastern Asia. The aquatic insects of California are well treated by Usinger *et al.* (191). For lower California, Ross (166) reports that of 14 species of Trichoptera, four are widespread through much of North America, four are known from widely separated localities in the Southwest, two are known from western California, and four are endemic. Of the latter, one is of Rocky Mountain relationship and three belong to the southwestern fauna and might be found in Mexico.

Neotropical.—Connections between North and South America, according to Ross and King (169, 170), were one in mid-Cretaceous and several between the Eocene and present, with two successive partial bridges in late Oligocene and lower Miocene, but also long periods of separation of the two continents. This permitted much specialization in South America. Speciation of some butterflies and moths on islands of the Antilles is discussed by Munroe (139, 141). For one group of pyralids, three waves of immigration are cited. Large size, great north-south extension, and very slight submersion of South America gave much opportunity for movement in times of changing climate, permitting preservation of ancient types, as well as diversification [Malaise (122)]. Many living groups appear to have originated there. Zonation in Bolivia is treated by Forster (58), who shows the distinct separation of environments, largely by altitude. Ringuelet (163) discusses the faunal rela-

tions of the southern Cordillera in Argentina. Neotropical and Ethiopian relationships are discussed by Mayr *et al.* (133).

Schweiger (176) discusses beetle distribution in southern South America, in relation to the subantarctic islands, showing that much of the area was not covered during ice ages. He states that Andean forms are found in Tierra del Fuego and that the Falkland Islands fauna differs from that of Tierra del Fuego in lacking xylophagous species. Brinck (17, 18, 19) shows that with the beetle faunae of South Atlantic islands, aside from cosmopolites brought by man, the species largely belong to endemic genera and many are flightless. In the absence of land connections, ancestors of all of these must have been brought by winds, but the land and fauna may have been more extensive earlier. He points out that most of the sub-antarctic beetles are phytophagous, whereas most subarctic beetles are carnivores.

Galapagos beetles are treated by Van Dyke (195), showing ancient derivation from barren grounds of Ecuador and Peru. He believes they are continental islands isolated by subsidence, but most workers consider them oceanic. Wirth (207) treats some Juan Fernandez Diptera, making comparisons and demonstrating flightless species.

Ethiopian.—Most people draw the northern border along the south edge of the Sahara, and eastward to include southern Arabia. Oldroyd (146) in treating Ethiopian Tabanidae states that the group arrived in Africa both from north and south, the primitive ones from the latter. He favors the Gondwanaland theory, but states that he has no new evidence for it, and that continental drift need not be invoked if there was a larger Antarctic continent. Uvarov (192, 193) shows that species on high African mountains are not related to European species, and are old elements, possibly from central Asia. He says that southward migration from Europe is not applicable in African acridiids, and that the Sahara was encroached upon by Ethiopian savannas, which left relicts in oases, rather than having been cool enough in the Quaternary Pluvial to permit north-south migration of Mediterranean or northern forms, as suggested by Jeannel.

Madagascar is generally considered a strong subregion of the Ethiopian Region, but sometimes separated as a Malagasy Region [Emerson (49)] or "Lemuria." Paulian (152) discusses the insects of Madagascar, stressing the highly endemic, initially disharmonic, yet diversified fauna. He states that the Mascarenes were never connected with Madagascar, and obtained their insects by over-sea dispersal. Madagascar was connected to Africa in mid-Jurrassic but, according to Delamare Debouttéville and Paulian (39), it has been impossible to prove a connection between Madagascar and India. The Mascarene fauna is oceanic, disharmonic, and influenced by Madagascar, according to Viette (198), and the Reunion fauna is similar to that of Mauritius, but the two islands were never connected. Vinson (199) shows that in the Carabidae, Mauritius has 41 per cent endemism, Reunion 39 per cent endemism, and Rodriguez no endemism. Indications of discontinuous distribution between Pacific and Indian Ocean islands is presented by Delke-

skamp (40), Gressitt (72), and Fennah (54). Some of these cases undoubtedly involve the preservation of primitive forms as a result of lack of competition on oceanic islands, with the forms having become extinct in continental portions of their former ranges.

Oriental.—The mountains of West China and Himalaya are among the oldest and best preserved Tertiary relict areas. The higher mountains, including those in Burma, South China and Taiwan, fall within the Palearctic Region, as there is no barrier in the east. Caradja (28) discusses some of these problems. India was an island until towards the Pleistocene [Malaise (122)].

In considering mosquitoes, Lee & Woodhill (110) place the boundary between the Oriental and Australian regions between the Lesser Sunda Islands and Celebes on the one hand and the Moluccas and Timor on the other. They point out that most of the Australian species are in the north and east, which seems to suggest recent Oriental intrusion, and that the Papuan area might form a very strong subregion of the Oriental Region, and include the species in Australia. There are a number of groups which show very conspicuous Philippine-Papuan distribution, extending into Micropolynesia, but with practically no representation in the Sunda Islands or Australia (72, 126). Some of these continue on in part to New Zealand through New Caledonia. The question of this Oriental-Australian boundary is discussed by Mayr (132) who cites percentages of representation of Oriental and Austral-Papuan faunae, based only in small part on insects. Southeast Asia and the Malay Archipelago were land at the end of the Mesozoic, alternately connected with the New Guinea area, while southern New Guinea was connected with Australia. At that time perhaps, and even up to the Pliocene, central New Guinea was beneath the sea and the rest consisted of strings of islands, with more extensive land to the north where the Bismarcks and Solomons are, and farther west (73, 168, 189). An outer Melanesian arc extended eastward to the New Hebrides, and perhaps closer to Fiji than at present, but only as islands. The inner Melanesian arc extended to New Zealand, and may have existed in the Cretaceous and been of short duration.

Although the mammals of New Guinea are Australian, many groups of insects show more distinct Asian origins, derived largely before the development of higher mammals. Then occurred a long isolation from Australia during the Tertiary, until the Pleistocene interchange. New Guinea has a highly autonomous fauna, with almost no true temperate Australian or northern alpine elements in many groups (189). Oriental groups extending through New Guinea to the Solomons or Fiji, or groups concentrated in the Philippine-New Guinea area, are lacking in Australia or found there only in North Queensland (126, 189, 196 and others). Wilson (205, 206) demonstrates that in the case of the ants, New Guinea has mixed Indomalayan, Australian and endemic elements, with none predominating, and that the New Caledonia fauna is close to that of Australia. This more nearly approaches the situation in birds than in the above cited examples.

New Guinea has been placed in the Australian Region by many (e.g., 38, 200), in the Oriental Region (72, 73, 189), as a separate Papuan Region more closely related to Oriental than Australian (49), and as a zone of equal mixture of the Oriental and Australian regions (42). Hennig (80) refers to the Oriental-Papuan Region.

Samoa's insect fauna is reviewed by Buxton (27), who shows its oceanic, disharmonic fauna, related to continental areas to the west through Fiji. Kaszab (97) calls Fiji continental, but I (72) feel that its disharmonic fauna is oceanic. Esaki (50) considered Palau, Yap and Fiji to be continental islands and part of the Melanesian Subregion. I (72) have treated all the islands north and east of the Solomons, to Hawaii and Easter Island, as Polynesian and oceanic, placing Hawaii and New Caledonia in special subcategories of their own. Many workers have also considered these islands primarily Oriental in their relationships, while apparently leaving New Guinea, the source of much of the fauna, in the Australian Region. Zimmerman (208, 209) treats the faunae of southeastern Polynesia and Hawaii, and Gressitt (70, 72), Micronesia and Pacific islands in general. Lord Howe Island is oceanic and has mixed elements, many of them probably derived from the ancient Inner Melanesian island arc. Lord Howe's fauna is discussed by Paramonov (149).

Australian.—Riek (162) presents some information on Australian fossil insects supplementary to Tillyard's extensive work, and sheds some light on past climatic conditions and faunal changes. When the northeastern part of Queensland is excluded as part of the Oriental Region, the insect fauna of Australia stands out in most groups as extremely distinct from other regions, except for moderate recent interchange with New Guinea and some archaic groups shared with the other southern continents.

In many respects the New Zealand fauna is quite distinct from that of Australia, with little recent interchange. Salmon (171) shows how the connection between Australia and New Zealand must have been a northern one, and never direct, and Ross (168) demonstrates immigration to New Zealand via the Inner Melanesian island arc, from New Guinea through New Caledonia. In treating the insect fauna of the subantarctic islands south of New Zealand, Hudson *et al.* (87) assume that Antarctica was connected to Patagonia and New Zealand. It may have been that Antarctica and the intervening islands were once larger, as well as more temperate, but that insects were exchanged by air dispersal over narrower sea barriers, which were sufficient to prevent migration of land mammals. Lane (107) does not require an antarctic connection.

Leclercq (109) suggests a migration route, not necessarily continuous land. He discusses the temperature of the Bering bridge, and the possibility of ancestors having been more temperature-tolerant than descendants. Malaise (123) hypothecates a land bridge across the South Pacific from New Guinea to South America to explain some relationships found in the Malay area,

New Guinea, and South America, but not in Australia. More likely, however, these crossed over the Bering bridge. Malloch (124), is somewhat skeptical of a southern connection, indicating that if it existed, it must have been before the evolution of calyptrate Diptera. Mackerras (120) also discusses southern relationships from the standpoint of Diptera, without reaching conclusions as to the mode of dispersal.

Distribution of Insect Groups

Collembola.—Salmon (171) discusses dispersal factors in Collembola, showing the New Zealand fauna to demonstrate northern connections with Asia and Australia, but possibly also a source of Antarctic fauna, though he disfavors the idea of a major Antarctic continent or Gondwanaland. He suggests a northern origin for the order.

Ephemeroptera.—Edmunds (44) discusses the very close relations between Australia, New Zealand, and southern South America, with four subfamilies, each with one or more representatives in each of these three areas.

Odonata.—Frazer (60) treats relationships of part of the Ethiopian fauna. Laidlaw (105) shows that the Ceylon species are 57 per cent lowland Oriental or Paleotropical, 18 per cent related to Indian species, but differentiated through isolation. The remainder are related to forms in Burma and Malay, carried by monsoon winds, or spread in Pleistocene times when climate was different along coasts of the Bay of Bengal. Lieftinck (112) discusses the replacement of races among two sympatric species showing differing abilities to overcome various barriers, the younger species jumping over niches of the older.

Plecoptera.—Some notes on world distribution of Plecoptera are given by Ricker (161), who shows that some of the primitive groups are southern. The distribution of the European *Isoperla* are treated by Illies (89) in terms of evolution and ecology.

Orthoptera.—The distribution of the Grylloblattidae, a Holarctic, or Amphiberingian, group has been treated by Gurney (75), who shows that both species and genera are very limited in range. For the Mantodea, Beier (6) states that it is a tropical group, with one endemic subfamily in Australia, and the Neotropical fauna very distinct from that of the Old World. Ragge (156) discusses the spread of some tettigoniid genera through South Asia, into Indonesia and the Philippines. Rhen (158) cites North America as area of origin of some groups of acridiids.

Isoptera.—Termite zoogeography has been admirably worked out by Emerson (48, 49) who shows that the distribution of this old group, which has several cosmotropical genera, can be explained without reference to continental drift or land bridges except between adjacent areas such as the Bering Straits. He shows that Australia was isolated from Malaya at the end of the Mesozoic, before the subtropical Bering migration route from Malaya to South America was cut off, that the Oriental Region was a

general area of exchange between most of the other regions, and that exchange between North and South America took place before early Eocene and after late Pliocene.

Psocoptera.—Gurney (74) and Mockford and Gurney (137) have discussed psocids common to Europe and North America, stressing the role of air currents in the distribution of these insects.

Thysanoptera.—In analyzing the distribution of thrips of east central Europe, Oettingen (145) shows that many are steppe species, some prairie species, fewer are forest species, a few are limited to specific hosts, and quite a number are of Palearctic or Holarctic distribution. Stannard (183) shows that the thrips fauna of the prairie peninsula in midwestern United States differs from that of the Great Plains and that this is based on poor ground drainage as a result of glacial deposit.

Hemiptera.—Zoogeography of Homoptera has been discussed by Metcalf (134). Fennah (54), in treating Micronesian Fulgoroidea, shows that the group entered the area mainly from the west through Palau, but also in the east from the Solomons, and stresses the need for host and other data to determine why some groups repeatedly colonize islands and others fail to. Evans (51) discusses the evolution and spread of the different groups of Jassoidea for the world on the basis of continental drift. The Psyllidae of the Australian Region are treated by Harrison (78), who cites several waves of immigration, including Tertiary influx from Malaya. Tuthill & Taylor (190) revise some of this work. For the scale genus *Kermes*, Balachowsky (4) shows that all 40 species are Holarctic and most of them are on oaks, often limited to one species or species-group of host.

For Heteroptera, the aquatic fauna of Syria and Iran is indicated as predominantly Palearctic, by Brown (23), with more Eurosiberian elements than Mediterranean and Sahara-Sind elements combined, and the constitution similar to that of Turkey except for a slight Ethiopian intrusion. Jordan (96) considers Heteroptera (except Corixidae and Miridae) good zoogeographical indicators because of their weak flight and their habitats.

Trichoptera.—Several very valuable discussions of caddisfly dispersal and evolution are presented by Ross (165 to 168) and Ross and King (169, 170). For *Atropsyche* (170) it is shown that the most primitive species occurs in the Mexican Plateau (and this is probably the area of origin), but that it arose from an Eurasian ancestor reaching Central America in late Cretaceous, becoming segregated into North and South American segments which were separated during the Eocene, the North American segment being *Atopsyche*. Later connections of North and South America permitted two-way crossing of species groups, some of which developed from immigrants from North to South America. In treating three families of cool-adapted caddisflies, Ross (168) shows that they are primarily Holarctic, but occur elsewhere in mountains and in temperate southern areas, only one group in each family becoming warm-adapted. He shows that there are sufficient fossils and enough survival to trace evolution and spread. He ascribes major dispersal to the

Bering bridge and finds no indication of dispersal between Australia and South America, except in one group where another explanation proves just as satisfactory.

Lepidoptera.—Considerable discussion of geographic subspeciation in Lepidoptera is presented by Remington *et al.* (160). Distribution of Greenland Lepidoptera is treated by de Lesse (111), who shows that of 36 species, 22 are Holarctic, six in North America but not in Europe, two in Europe but not in North America, and six endemic. Brachypterous jumping flightless moths of islands south of New Zealand are treated by Hudson *et al.* (87) and Salmon & Bradley (172), although fully winged endemic species are also present. The microlepidoptera of central New Guinea are treated by Diakonoff (42), who states that the faunae of neighboring regions are too little known to make satisfactory comparisons, but the fauna seems to represent the result of somewhat equal competition between Australian and Oriental elements. In the pyralids, Box (14) discusses changes in distribution relating to changes in hosts, as from grasses to cane, among others, and the effect on native parasitic wasps. For the Nymphaulinae, Lange (108) analyzes the world distribution, showing that the Australian and Oriental Regions are richest, the group having a tropical origin, with few adapted to cold conditions. For Kashmir agrotids, Boursin (13) indicates four elements: (*a*) West China-Himalayan, (*b*) suberemic Eurosiberian, (*c*) endemic (possibly relicts of Pamir fauna), and (*d*) subtropical Oriental. Spreading back and forth of lines of Saturniidae between Asia and North America is discussed by Michener (135). The larger moths of Rennell Island are shown by Fletcher (55) to have come largely from the Louisiades, secondarily from the Solomons or Bismarcks.

The ecological zoning of butterflies in Bolivia is treated by Förster (58). Distribution of the *Euploea* butterflies on Pacific islands is discussed in detail by Carpenter (29). He indicates general agreement with Mayr's conclusions for the birds of the area, but states that relations between species in the Moluccas and Solomons proves continental drift, but this can be countered by evidence of former more extensive land area to the immediate north of New Guinea. It can apparently be inferred that the Australian species are recent Pleistocene immigrants. Hoffmeyer (83) shows that the Danish macrolepidoptera entered from the east during the past 10–12,000 years. Mexican and Antillean Papilionoidea are treated by Comstock & Huntington (32). The arctic-alpine North American *Erebia* are discussed by Ehrlich (47), particularly as to barriers to dispersal. The distribution of arctic and subarctic butterflies is considered by Freeman (62). Oriental elements in eastern Palearctic butterfly distribution are discussed by Shirozu (180).

Diptera.—Mackerras (120) gives an excellent discussion of the zoogeography of Diptera, mainly working from the standpoint of the Australian fauna. Séguy (178) presents a general review of the world distribution. He recognizes a Malagasy Region and separates Oriental and Australian between the Moluccas and New Guinea. World distribution is also treated by

Hardy (77), who shows that many families are primarily tropical, but that the Apioceridae, Pelecorhynchinae, Ceratomerinae groups of Leptidae and Chiromyzidae are found primarily in Australia, Tasmania, New Zealand, southern South America and South Africa (all with larvae in swamps or damp soil), and relates this distribution to continental drift. Hennig (80) treats Diptera distribution as divided into two types, Holarctic and southern, stating that they show that existence of Gondwanaland until Triassic explains elements in common between Africa, South America and Australia, but that there were also upper Cretaceous and older Tertiary connections between Africa and South America.

The world distribution of Culicidae is tabulated by Lane (107) who shows that the Neotropical and Australian Regions are richest, the former demonstrating connection only with Nearctic and the latter only with Oriental, with Nearctic and Palearctic not very distinct. He states that haematophagia is not related to dispersal. Edwards (45) and Mattingly (129) outline African mosquito distribution. Edwards shows that the Ethiopian mosquitoes have much in common with those of the Oriental Region as far as genera are concerned, although more species are possessed in common with the Palearctic Region. There is little in common with the Neotropical Region except cosmopolitan genera. Mattingly classifies 17 districts in six provinces of two subregions, mainly following Chapin's system for birds. Mattingly and Knight (130) treat Arabian mosquitoes showing that the mosquito fauna of Arabia corresponds with that of the birds, in that the southern portion is Ethiopian and the northern is Palearctic, with a narrow strip of Oriental Region on the opposite coast of Iran, beyond which is Palearctic again. Iyengar (90) treats distribution of South Pacific Culicidae, dividing the islands into northern (Micronesia), eastern (Samoa, Tonga, Ellice, southeastern Polynesia), intermediate (Fiji, New Hebrides, New Caledonia), and western (New Guinea, Solomons) areas. The distribution of South Pacific species from the ecological standpoint is treated in detail by Laird (106), who points out that *Anopheles*, which is not found south and east of Aneityum, New Hebrides, could establish in Fiji and Samoa, but not in New Caledonia. Australasian *Anopheles* distribution is treated by Lee & Woodhill (110). For Micronesian mosquitoes, Bohart (12) indicates 62 per cent species endemism, no endemic genera, and relationships dominantly Oriental proper and secondarily Papuan. Belkin (8) treats southwest Pacific mosquitoes. Alaskan mosquito distribution is referred to by Frohne (63) who emphasizes the short season, cold tolerance, habitats, and life cycle modifications of these insects.

The Ethiopian Simuliidae, according to Freeman & de Meillon (61) comprise a distinct fauna, which is controlled by available habitats, and consists of an east and west part, with Madagascar separate but with links with East Africa, vague links with Australia, but none with the Orient. Nearctic simuliid patterns were studied by Shewell (179) and Alaska ecology and distribution by Sommerman *et al.* (182). In discussing "Australasian"

Phlebotomus, Fairchild (53) points out the relative lack of diversity as compared with the Neotropical representation, and also mentions that so far no members of the genus have been found in Chile. The occurrence of chironomids in old lakes of southern Sweden is considered in detail by Brundin (26). The history and spread of *Culicoides* is reviewed by Khalaf (98) who feels that many groups evolved in the Oriental Region, or farther north when climate was warmer.

The history of the spread of tsetse flies is treated by Evens (52) on the basis of Jeannel's Wegenerian patterns. He believes that they are of a possible Angara rather than Gondwana source, and shows that the pupal diapause indicates a cool-climate origin. In an excellent study of Tabanidae, Mackerras (121) treats history of distribution, mentioning Gondwana and Antarctic faunae, but not drift or bridges. He speaks of a southern distribution of primitive forms, and for specialized groups, of both a southern regional radiation and a northern radiation like that of Eutherian mammals. Oldroyd (146) gives a fine treatment of the Ethiopian distribution. Philip (154) discusses Mackerras' and Oldroyd's ideas in a generally favorable vein. For Tephritidae, Hering (81) shows that proportional representation of Tephritinae and Trypetinae changes somewhat between Indonesia and New Guinea. Drosophilid distribution is discussed by Patterson and Wheeler (151). Roback (164) attempted to correlate phylogeny and distribution of Sarcophaginae of the world, in connection with a Nearctic study.

Siphonaptera.—The northern Nearctic flea distribution, according to Holland (85), shows that not all species have the same range as their hosts, and that some of the Holarctic species are limited in the Nearctic to the part of the Alaska-Yukon area that was ice-free at the height of the Pleistocene.

Coleoptera.—For Carabidae, Darlington (35) has shown that selection for flightlessness is related to size of area and the reduced usefulness of wings on mountains and islands, and demonstrates similarities in these two types of environments. For the New Guinea Agonini, Darlington (37) shows that most of the genera are endemic but probably had an Oriental origin, besides those which are clearly Oriental or widespread. Britton (22) states that the tribe Broscini demonstrates a Cretaceous Palaeantarctic origin, and that the group reached South America by way of a southern land connection. From there it traveled to Africa across another bridge, but could not have reached Asia because the latter was separated from the southern areas from late Jurassic till late Tertiary. Ball (5) states that the Broscini distribution can prove nothing about former land connections, and that geological evidence is against a direct land connection between South America, Antarctica, New Zealand and Australia. The paussids, according to Darlington (36), are mainly tropical, poorly represented on islands, fairly young as a group and not pre-Jurassic. They were not distributed by continental drift as claimed by Jeannel, or by an Antarctic land bridge as claimed by Kolbe. Janssens (91) disputes some of Jeannel's conclusion on paussid distribution. Jeannel has used the Pselaphidae also in explaining distribution by continental drift

(94). Park (150) and Schuster & Marsh (175) treat ecological factors governing distribution and phylogeny of Pselaphidae. For Australian gyrinids Brinck (20) feels the distribution offers no indication of migration between South America and Australia, as suggested by others, but, rather, old and recent exchanges with Asia. For South African gyrinids Brinck (21) indicates a purely Ethiopian fauna, with no connections to South America or Australia, and with endemic centers in the southwest and southeast, probably representing refuge areas in periods of drought.

For Erotylidae, Delkeskamp (40) shows that most species are in only one region. The Neotropical region is richest and most primitive, and the Madagascar fauna is Ethiopian. The Chinese Cassidinae demonstrate a filter-bridge barrier during the later Bering connections of New and Old World and correlation between evolution of the beetles and their host plants [Gressitt (69)]. Chinese Cerambycidae (68) demonstrate the mixing of Palearctic and Oriental elements, and the striking contrast between the fauna of the Philippines on one hand and Hainan and Taiwan on the other. Micronesian cerambycids (71) show a disharmonic fauna lacking many of the dominant tribes in the Philippines and New Guinea, and possessing largely oceanic genera including some flightless endemic genera and species. Distribution of North American Cerambycidae is treated by Linsley (118). The Balearic Chrysomelidae [Jolivet (95)] shows the islands to be continental and to demonstrate Miocene connections with Corsica and Sardinia or Sicily, and Pliocene connection with Spain. Tenebrionidae of the Thar Desert of North India are shown to be related to the Baluchistan and southern Persian faunae by Kulzer (104). The weevil tribe Celeuthetini [Marshall (126)] shows a very distinct Philippine-Papuan distribution, spreading into Polynesia. The Cossoninae are described by Peyerimhoff (153) as well developed on oceanic islands, but not on Madagascar.

Hymenoptera.—Distribution and history of Tenthredinoidea is treated by Malaise (122), who invokes land bridges, but not continental drift. Orussid distribution is treated by Benson (9). The origin of *Cynips* in Mexico is shown by Kinsey (99), with two lines, one of which spread to Eurasia, probably in the Oligocene. Stohl (184) in outlining distribution of Gasteruptionidae, states that some forms of primitive appearance may actually be more advanced physiologically. Brown (25) discusses the stages of tramping of ants through human agency, pointing out that most tramp ants seem to be of African origin, and some of them have become dominant on islands, as in the Indian Ocean, through lack of competition, and were spread thence to other areas. Brown (24) feels that the distribution of the Dacetini can be accounted for by separate waves of dispersal centered in the Old World tropics, each major wave representing a genus or species-group in the present classification. Each genus or group tends to replace the preceding one from the central area outward. Some of the older waves are now represented only by specialized relicts surviving in peripheral areas or in particularly favorable, but limited, habitats. For the Scoliidae, Betrem (11) indicates waves of

southward migrations, prompted by the ice ages, from both India and China into the Malay area, and Bradley (15) indicates primitive ancestors in Palearctic Africa and in Madagascar, and also a tendency for wing coloration characteristic of different parts of Africa among many species. The distribution of Zethini and Eumenini in the eastern Mediterranean area is compared with that of other groups by Giordani Soika (64) and the elements shown to be Mediterranean, Saharo-Sind, endemic Palestine, Irano-Turanian, Sahelo-Sudan and Eurosiberian, in order of decreasing representation. For the Crabronidae, Leclercq (109) indicates a definite Holarctic fauna, and clear Australian-South American relationships. Moczar (138) treats faunal elements of Carpathian pompilids. Some melittid distribution is treated by Popov (155). Malyshev (125) and Michener (136) treat distribution of bees. Maa (119) shows that the honeybees are eurythermous and that their primary distribution center is the Malaysian Subregion.

Arachnida.—Opiliones of Chiapas, Mexico, show unclear patterns but roughly fit in three zones, north bulge lowlands, high central mountains, and Pacific slope lowlands, [Goodnight & Goodnight (67)]. Hoogstraal (86) treats tick distribution in the Malagasy area. Wharton & Fuller (203) show that trombiculids are best represented in Australia, southern Asia, Africa and adjacent islands. Some genera are widespread, and some may have originated outside the above area.

Myriapoda.—Some data on Newfoundland myriapods is presented by Palmén (148).

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HYBRIDIZATION AND SPECIATION IN MOSQUITOES[1]

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The importance of mosquitoes as pests and disease vectors has caused the Culicidae to be one of the most thoroughly studied families of insects. A number of groups containing closely related species or subspecific populations have been described. Some of these represent special problems to the epidemiologist, who is faced with the necessity of distinguishing between morphologically similar species in order to understand their respective roles in disease transmission. An example is the many references in the older literature to "anophelism without malaria." These species complexes are of special interest to taxonomists and a few geneticists who find in them opportunities not only for additional descriptions, but for investigation of evolutionary processes leading to speciation.

There are several methods for studying these processes. Systematic work is of value in that it often reveals the existence of such species complexes. Sibling species represent a fertile area for the study of the mechanism of speciation and evolution. Ecological and comparative physiological research may demonstrate existence of biological divergences. However, morphological and biological discontinuities between populations must often be interpreted subjectively by the investigator, and we are still faced with the necessity of depending upon the judgment of the specialist for arranging the populations in their phylogenetic perspective. Sterility barriers would appear to be positive evidence of divergence to species rank, while interfertility often indicates subspecific status. Although these criteria do not apply to all cases, a body of knowledge built up through hybridization experiments should show to what extent fertility and mating barriers can be applied to solution of taxonomic problems. But hybridization experiments are of special importance in that it is only through genetical and comparative biological studies that we will be able to understand the evolutionary mechanisms leading to divergence.

Only a few of the mosquito population groups have been utilized in hybridization and other genetic investigations. Kitzmiller (25) has presented a review of work done up to 1953. The purpose of the present paper is to summarize the work that has been done since 1953 on speciation in mosquitoes; however, it will be necessary to refer to some of the older papers. We

[1] The survey of the literature pertaining to this review was completed in May, 1957.

shall also attempt to draw certain conclusions regarding the findings with respect to speciation among mosquitoes, and finally, to present some ideas concerning the possible significance of the evolutionary speciation mechanisms to certain practical problems in medical entomology and public health.

The *Culex pipiens* Group

The common household mosquito is represented in various parts of the world by populations which have been given specific or subspecific names. Those with which we are concerned are as follows:

Culex pipiens pipiens Linnaeus has a palaearctic distribution and is also found in certain other areas such as Australia and more elevated regions in East and South Africa. Within this broad range, populations have been designated as subspecies of *pipiens*, but their position is as yet uncertain. These include *pallens* Coquillett of the Oriental Region, *australicus* Dobrotworsky and Drummond in Australia, and *berbericus* Roubaud in N. Africa.

Culex pipiens fatigans Wiedemann (*quinquefasciatus* Say) replaces *pipiens* in the tropical and subtropical regions of the world, and in many areas its range overlaps that of *pipiens*.

Culex molestus Forskål occurs in many localities within the *pipiens* range. This name is being used in this paper as a convenient designation for populations, morphologically identical with *pipiens*, which are distinguished by an ability on the part of females to deposit eggs without imbibing blood or any other food. The taxonomic position of *molestus* is uncertain. We consider *Culex autogenicus* Roubaud, and races *sternopallidus* Roubaud and *sternopunctatus* Roubaud, to be synonyms of *molestus*. For a summary of Roubaud's interpretation of these forms, the reader is referred to a recent paper by this author [Roubaud (46)].

Culex globocoxitus Dobrotworsky has been described from Australia.

No consistent biological differences between *C. p. pipiens* and *C. p. fatigans* have been found. The only morphological distinction between *pipiens* and *fatigans* is seen in the DV/D ratio, which is a measure of the angle of inclination of the ventral arms of the mesosome. In a recent study, Barr (2) has shown that *pipiens* exists in North America as a cline; the DV/D ratio is smallest in more northern populations and increases progressively in the populations towards the south. In a broad belt from 36 to 39° N. lat., where overlapping of the two populations occurs, Barr found evidence of hybridization and mixing. He noted that in Sacramento County, California, thorough intermingling occurs. Galindo (17) states that "a great deal of interbreeding takes place between *molestus* and *quinquefasciatus* in California." Bekku (3) has compared *pipiens* populations from several regions in the Orient, and concluded, "The Japanese house mosquito belonging to the *pipiens* group which is distributed all over Japan from Kyushu to Hokkaido should be regarded as a hybrid population of *pipiens* and *fatigans*. . . . " His findings support the views expressed some years ago [Free-

born (13); Rozeboom (48)] that *pallens* is a widespread hybrid population in the Orient. Hybridization in nature confirms our earlier conclusions that *pipiens* and *fatigans* should be regarded as subspecies; nevertheless, in many regions they appear to maintain their respective identities. Although gene flow may be quite free between different populations in certain areas, Barr found that in most places in North America the parental forms are more common than the intermediate, "which suggests that there may be unrecognized isolating mechanisms present." In this they may be aided through adaptations to their environments. One might expect them to show differences in responses to temperature, but as yet these have not been demonstrated, with a possible exception in mating activity [Farid (11)].

Culex molestus has been described as differing from *pipiens* and *fatigans* in being man-biting, able to mate in small spaces (stenogamy) and capable of breeding through the year without going through diapause (homodynamy). None of these characters appears to be diagnostic. Möllring (42) and Twohy & Rozeboom (59) noted that *molestus* larvae require a day or two longer than do *pipiens* larvae to complete their development. Possibly as a result of this longer period, *molestus* larvae grow to larger size. The adults of *molestus* are far more active sexually than are *pipiens* and *fatigans*. Under conditions which permitted only 19 to 33 per cent insemination of *pipiens* or *fatigans* females by their own males, 92 to 95 per cent of the *molestus* females were fertilized by their own males [Rozeboom & Gilford (50)]. This greater sexual activity is possibly the basis for the characterization of *molestus* as being stenogamous.

The only clear-cut difference between *molestus* and the other *pipiens*-group populations is in the ability of the females to lay eggs without having fed in the adult stage. Such autogenous eggs are produced from food reserves accumulated in the larval stage, and it has been suggested that the richness of the larval diet would be the determining factor. In a recent histochemical study of the fourth stage larvae, Clements (8) concluded that although the fat body in *pipiens* is less extensive than in *molestus*, the former does contain "a considerable amount of reserves," and that enough reserves were carried over to the adult *pipiens* in the fat bodies and abdominal muscles to permit a number of eggs to develop. Twohy & Rozeboom (59) made comparative quantitative determinations of lipides, glycogen, and nitrogen in female pupae and adults of *molestus* and *pipiens*. They found that *molestus*, being a large mosquito, contains more proteins per individual than does *pipiens*, but in terms of protein per mg. dry weight, the proportion of proteins was greater in *pipiens* than in *molestus*. Lipide and glycogen reserves are greater in *molestus*, but their rates of utilization are the same in both mosquitoes. Ova in *molestus* begin to grow by the second day after emergence from the pupa. At this time, *pipiens* females still contain fair amounts of food reserves, although the follicles do not develop beyond the deposition in the oocyte of a few granules which we presume to be yolk, or a yolk precursor. It would appear then, that all of the reserves in *pipiens* are destined from

the very first to be utilized entirely as an energy source for the adult female. Clements (8) showed that ovarian development in *molestus* could be prevented by decapitation of the adult female earlier than seven hours after emergence, or by ligation at the base of the abdomen earlier than five hours after emergence. Decapitation or ligation after the above periods permitted partial or complete development of the follicles. Clements was unable to stimulate ovarian growth in *pipiens* by transplanattion of brains, corpora allata, or corpora cardiaca from *molestus;* nevertheless, the evidence at least suggests the presence of a gonadotropic hormone in *molestus*. It is also possible that a specific food factor is utilized or synthesized by *molestus*, which acts either on the neurosecretory glands or directly on the ovaries.

A conclusion to be drawn from the above observations is that *molestus* is not a seasonal or phenotypic variant of *C. pipiens pipiens*, but is inherently a physiologically different form. The differences are very striking, and would appear to be far greater than those we see between *pipiens* and *fatigans*. The question then arises as to whether the autogenous form represents a different population which maintains its identity in nature. To study this problem, it is necessary to understand the mechanism of inheritance of autogeny. Roubaud (44), who first showed by crossbreeding of *molestus* and *pipiens* that autogeny was under genetic control, concluded that the character was inherited as a simple mendelian recessive. Subsequent work has not confirmed this, and in the most recent study on the inheritance of autogeny, Spielman (54) showed that there was a direct correlation between a chromosomal dosage for autogeny in his experimental hybrids and penetrance and expressivity of this character. Utilizing the information that *C. pipiens* has three pairs of metacentric chromosomes, and that sex is determined at a single locus at which maleness is dominant [Gilchrist & Haldane (20)], it is possible to set up five hypotheses with respect to inheritance of autogeny. One, two, or three factors may be involved, and in the first two there may or may not be linkage with the sex chromosome. In a series of 14 crossbreeding and backcross combinations between *molestus* and *pipiens* or *fatigans*, there was a continuous relationship between chromosome dosage and appearance of autogeny. Autogeny was not inherited as a simple recessive or dominant; F_1 hybrid progenies were intermediate, and the percentages of autogenous individuals in the various progenies were related to the numbers of autogeny-bearing chromosomes introduced. Statistical treatment of the experimental results showed that the observed values best fitted the hypothesis that autogeny factors were carried on each of the three chromosomes. During the course of this work, a spontaneous yellow larval mutant occurred in the *molestus* colony; this was bred selectively until an autogenous strain homozygous for yellow color was obtained. This character was inherited as a simple mendelian recessive. Crossbreeding of the autogenous yellow strain with dark-colored *fatigans* produced F_2 and backcross hybrids in which there was a random assortment of color and sex; nor was there a

linkage between autogeny and yellow color. This would suggest that although the three factor hypothesis was in closest agreement with the observed data, one of the chromosomes does not carry an autogeny factor. However, since some of the autogeny genes are sex-linked, the most reasonable assumption to be drawn from Spielman's results would appear to be that autogeny is inherited on two chromosomes, one of which also carries the sex factor. Spielman notes that crossovers may occur between some of the factors for autogeny and sex. Although the actual number of genes could not be determined, nor could the chromosomes be identified, the degree of autogeny exhibited by the experimental hybrid populations representing known cross and backcross combinations, should serve as a measure for estimating the amount of interbreeding occurring in natural populations. Galindo's (17) conclusion, based on morphological evidence, that considerable intermingling occurs among *molestus* and *fatigans* in California, underscores the problem of the systematic relationships between *molestus*, *fatigans*, and *pipiens*. Do the genes controlling autogeny find expression only when the gene dosage for autogeny is large enough and under certain environmental conditions?

Some attempts have been made to determine the proportion of autogeny in wild populations. Knight & Abdel Malek (28) reared adults from larvae and pupae collected in natural breeding places in Cairo. They were held in cages for a 12-day period, and during this time only 1.1 per cent of the females deposited autogenous egg rafts. The surviving females were then given a blood meal. A few adults reared from the resultant eggs produced autogenous eggs. Thus, the factors for autogeny were present in phenotypically anautogenous females. In Australia, Dobrotworsky (9) collected larvae and pupae from natural breeding places, and kept adults emerging from them in cages for 20 days, during which time egg rafts were counted. The proportion of autogenous females ranged from 46.6 to 94.2 per cent in eight populations. One should note that it is important to determine not only the percentage of autogenous females among wild populations, but especially the relative proportion of autogenous genes possessed by individual females in wild populations. The latter information should tell us to what extent panmixia occurs.

Very few naturally occurring mutants have been observed among mosquito populations in nature or in laboratory colonies. These have included strains with yellow or green larvae and pupae [Huff (23); Ghelelovitch (18); Laven (33, 34); Spielman (54)] and white eye [Gilchrist & Haldane (20)]. The strains with yellow or green larvae and pupae may be made homozygous through selection, and crossbreeding experiments have shown that the factor for yellow behaves as a simple Mendelian recessive. White eye in *molestus* was shown to be a recessive character partially linked with sex. Nonviable, black larvae have also been observed. Kitzmiller (25) concluded that this condition is due to a three factor recessive lethal. Laven & Chen (34) concluded that the ratios of melanotic to normal larvae, which appeared in the

hybrids resulting from crossing of heterozygous and normal strains, show pigmentation and death to be due to an autosomal recessive lethal factor, which becomes manifest in the homozygous condition.

The apparent dearth of good "*Drosophila*-type" mutants in laboratory and natural populations of mosquitoes led Laven and Kitzmiller to attempt production of mutants by means of x rays. Laven irradiated males of *molestus;* Kitzmiller, males of *fatigans.* Both experiments were successful and led to somewhat surprising results.

Laven (30 to 34) described the following mutants:

(*a*) Rap—shortened antennae and palpi of both sexes, behaving as a dominant autosomal factor.

(*b*) kps—terminal segments of both palpi of males shortened and somewhat claw-like, behaving as an autosomal, recessive, sex-limited gene.

(*c*) Kpu—phenotypically similar to kps, except usually found in one palpus only, behaving as a sex-linked, sex-limited dominant.

(*d*) var—fusion of veins R_3 and R_{4+5} slightly before the wing margin, behaving as a sex-linked recessive.

Since his 1956 paper, Laven (personal communication) has also found the following mutants:

sch—scale row. An extra row of scales between veins R_1 and R_2. An autosomal recessive, expressed in both sexes.

Kuf—shortened wings. A dominant autosomal gene.

kfl—a spontaneous, recessive mutant causing shortened wings.

In addition to these morphological markers, Laven has discovered several other physiological genes controlling such factors as transformation of males into intersexes, and the hereditary production of gynandromorphs.

In a similar series of experiments Kitzmiller (unpublished results) has discovered the following mutants: (These are for the time being designated by name only, since several of them are strikingly similar to the phenotypes found by Laven. These similar mutants are now being tested for allelism, and genic designations are withheld until the identity or nonidentity with the German mutants is established.)

scale row—apparently identical in phenotype to Laven's mutant. An extra row of scales is present between veins R_1 and R_2. Extra scales also present in other areas of the wing. Inherited as an autosomal recessive.

symmetrically clubbed palpi—similar to kps in appearance but not consistent in genetic behavior. Behaves as a weak dominant, with low (15 to 20 per cent) penetrance.

unsymmetrically clubbed palpi—similar to Kpu, but genetic behavior not clear. May be identical with the above-described mutant.

closed R_2 cell—cell R_2 closed by a fusion of veins R_2 and R_3. Basic inheritance seems to be as a sex-linked dominant, but the picture is not simple. Occurs much more frequently in males.

cubital scaling—a strong patch of scales in the cubital area of the wing. Autosomal, recessive. Possibly a pleiotropic effect of scale row.

four jointed palpi—a striking sex-limited autosomal recessive, which when homozygous produces four-jointed palpi in the female.

spotted wings—a spot of black scales in the r–m crossvein area. An autosomal dominant of irregular behavior.

One importance of these findings is that by use of marked chromosomes it should be possible to determine the chromosomal location of physiological characters such as autogeny, insecticide resistance, susceptibility to parasites, and other traits which are of special biological or public health interest. Another striking feature of these experiments is the unexpected amount of parallel mutation and the extremely high mutation rate. These are items of importance to theoretical genetics and will be discussed elsewhere.

A number of authors have performed crossbreeding experiments with *pipiens*, *fatigans*, and *molestus* in order to ascertain whether genetic barriers might serve as isolating mechanisms. The results of several of these experiments are presented graphically in Table I. In the negative crosses insemi-

TABLE I

RESULTS OF CROSSING EXPERIMENTS BETWEEN STRAINS OF *Culex pipiens*, *C. fatigans*, AND *C. molestus* (11, 17, 24, 26, 27, 35, 47, 52, 54, 60)

Females		Males																						
		Illinois	Michigan	Maryland	S. Tunis	Alabama	Texas	Bakersf.	Fresno	Br. Guiana	Lagos	Brazzaville	Dakar	Noumea	Eritrea	Maryland	Oakland	Hamburg	Dremmen	Oggelshausen	N. Tunis	Cairo
		P	P	P	P	F	F	F	F	F	F	F	F	F	F	M	M	M	M	M	M	M
Illinois	P	+					+	+										+	–	–		
Michigan	P		+				+															
Maryland	P			+		+	+									+						
S. Tunis	P				+																–	
Alabama	F			+		+	+									+						
Texas	F	+	+	+		+	+															
Bakersfield, Cal.	F	+						+										+	–	–		
Fresno, Cal.	F								+								+					
Brit. Guiana	F									+	+											
Lagos, Nigeria	F									+	+											
Brazzaville	F											+	+									
Dakar	F											–	+									
Noumea	F											+	–[1]	+								
Eritrea	F														+							+
Maryland	M			+		+										+						
Oakland, Cal.	M								+								+					
Hamburg	M	+						+										+	+	+		
Dremmen	M	–						–										–	+	+		
Oggelshausen	M	–						+										–	+	+		
N. Tunis	M				+																+	
Cairo	M														+							+

P = *pipiens*, F = *fatigans*, M = *molestus*; + = successful fertilization with usually 50% or more of the eggs producing viable larvae; – = negative results with few larvae produced.

nation was successful, and sometimes as many as two-thirds of the eggs might contain embryos which were incapable of hatching, or died soon after hatching. The other eggs were not fertilized. While laboratory matings, taken by themselves, neither prove nor disprove the true taxonomic picture, they nevertheless do shed light on the presence or absence of inherent isolating mechanisms. If these various forms will cross in the laboratory, then some other isolating mechanism must be looked for if indeed, in nature, they exist as separate taxonomic entities.

Most crosses involving *pipiens*×*pipiens*, *pipiens*×*fatigans*, and *fatigans* ×*fatigans* have produced viable, fertile progeny; however, relatively few experiments involving these combinations have been tried. Some negative or partially negative results have been obtained [Weyer (61); Roubaud (45, 47)], but the ease with which most workers have been able to cross the American populations of *pipiens* and *fatigans*, plus the occurrence of natural intermediates has led to a rather wide acceptance of these two as subspecies. It is possible that strains of different geographic origin may prove to have real genetic differences. Roubaud (47) reported incompatability between *fatigans* females from Dakar and males from Brazzaville, and between New Caledonia females and Dakar males. He raises the question whether there might not be truly a *fatigans* complex with isolating mechanisms among various strains. On the other hand, Service (52) observed no genetic barrier between *fatigans* from Lagos, Nigeria, and British Guiana, and concluded that these two widely separated strains were conspecific. The preliminary results of crossbreeding experiments being conducted by Rozeboom between *fatigans* from Manila, P.I., and various strains of American *pipiens* populations have revealed no genetic barrier between the Manila strain and *fatigans* from Galveston, Texas.

The picture is more complicated when the data concerning *molestus* are taken into account. The results of the more important work are presented in Table II. Laven (29 to 32) has done the most extensive work, testing several *molestus* populations from Europe and North Africa. He finds that these populations fall into at least 10 groups, which differ from one another in their abilities to mate and produce viable, fertile offspring. The degree of isolation varies and is presumably of several different kinds. Some crosses will not succeed in either direction, producing only infertile eggs. Other crosses will succeed in one direction only. Still others will produce embryonated eggs which, however, fail to hatch. In these latter crosses, some few exceptional individuals are sometimes produced. Finally, some crosses succeed with ease, indicating no intrinsic sterility barrier. These *molestus* strains are all morphologically identical as far as can be determined but they certainly possess striking physiological differentiation. Laven has further clearly demonstrated (see below) that these differences are due to cytoplasmic factors present in each of the strains. These experiments were extended by Laven & Kitzmiller (35) to include comparisons between several European *molestus* populations, *fatigans* from California, and *pipiens* from Illinois.

TABLE II

RESULTS OF CROSSING EXPERIMENTS WITH STRAINS OF *Culex molestus* (19, 26, 29, 32, 35, 38)

Females	Males													
	London	Hull	Hayling Isl.	Antwerp	Paris	Eberfeld	Hamburg	Immenrode	Dremmen	Röhrnung	Oggelshausen	Mannheim	Sauri	Tunis
London	+	−	+	+	+	+	−	−		+	+	+		
Hull	+	+	+		+									
Hayling Isl.	−	−	+		−									
Antwerp	+			+	+	+	−	−		+	+	+		
Paris	+	+	+	+	+	+	−	−		+	+	+		+
Eberfeld	+			+	+	+	−	−		+	+	+		
Hamburg	−			−	−	−	+	+	+	+	+	+	±	+
Immenrode	−			−	−	−	+	+		+	+	+		
Dremmen							−		+		+			
Röhrnung	−			−	−	−	−	−		+	+	−		
Oggelshausen	−			−	−	−	−	−	−	+	+	+		
Mannheim	−			−	−	−	−	−		−	+	+		
Sauri							+						+	
Tunis					−		+							+

+ = successful fertilization with usually 50% or more of the eggs producing viable larvae; − = negative results with few larvae produced; ± = egg fertility of about 10 to 20 per cent.

The same type of result was obtained—some crosses were successful, others not, with the same kinds of sterility barriers evidently present.

A similar study in Australia was made by Dobrotworsky (10), with five *molestus* strains, *fatigans* and *C. globocoxitus*, another member of the complex. The results were much the same as in Laven's work; the strains differed in their abilities to produce viable, fertile offspring with one another.

In the above experiments, the presence of embryonated eggs is evidence of mating. However, another isolating mechanism could involve mating. In a series of mating selection experiments, Rozeboom & Gilford (50) demonstrated that differences in sexual activity were exhibited by North American *pipiens*, *molestus* and *fatigans* but that these differences did not function as barriers. Thus, when *fatigans* and *pipiens* females were in contact with *fatigans* males, significantly more *fatigans* than *pipiens* were inseminated by males, but the same was true when these females were in contact with *pipiens* males. Both sexes of *molestus* were especially active; more *pipiens* or *fatigans* females were inseminated by *molestus* males than by their own males,

while *molestus* females, in the presence of *pipiens* or *fatigans* females, tended to monopolize their own males as well as the males of the other two populations. Dobrotworsky (10) reports that no mating preference exists between Australian *fatigans* and *molestus*, or between several strains of *molestus*. The *molestus* and *fatigans* males did not inseminate *globocoxitus* females, but *globocoxitus* males fertilized the three kinds of females with equal readiness.

The data from these crosses clearly indicate that a great amount of genetic variability exists within *Culex* populations with respect to crossability and mating behavior. Some of the implications of this variability with respect to taxonomy and to genetics will be discussed below.

Laven's crosses with *molestus* deserve further comment. The varying degrees of incompatability among the different strains tested are clearly traceable to cytoplasmic factors. One example will illustrate the data. Strains of *molestus* from Hamburg (H) in northern Germany and from Oggelshausen (O) in southern Germany were crossed. The cross of an O ♀ × H ♂ was unsuccessful, but the reciprocal cross, H ♀ × O ♂, produced viable, fertile offspring. F_1 ♀s from the H × O cross were backcrossed to O ♂s. This standard genetic technique introduces more paternal type chromosomes (in this case from strain O), and after relatively few generations of backcrossing, always to O ♂s, the chromosomes should be entirely of the O type. The cytoplasm of all offspring, however, is largely derived from the original maternal strain, in this case H. Not satisfied with the 9 or 10 backcrosses which geneticists usually consider as sufficient for almost 100 per cent replacement of chromosomes, Laven backcrossed to O ♂s for 20 generations. At the end of this time, males and females of the 20th backcross generation were tested for their mating behavior. *In all cases, both males and females of the 20th generation showed crossing behavior like H individuals rather than like O*, in spite of the fact that the chromosomes were now presumably all of the O type. At this stage of the experiment the x-ray induced marker genes became available, and both H and O strains were marked in such a way that it became possible to state with certainty how many O-type chromosomes were in a given individual. The experiments have continued through more than 60 backcross generations with marked chromosomes, and the results remain the same—mating behavior like H rather than like O, in spite of the complete replacement of H chromosomes with O chromosomes. Many geneticists believe that this case is one of the most clear-cut demonstrations of cytoplasmic inheritance so far known.

The *Aedes scutellaris* Group

According to Marks (37) there are 18 species and subspecies in this group within the subgenus *Stegomyia*. Their combined ranges extend through the islands of the Pacific from the Tuamotus and Pitcairn in the Southeast, to Christmas Island in the Southwest, and through the Philippines to Okinawa in the Northwest. Within this insular distribution there should have been ample opportunity for the appearance of different populations as a result of

isolation. The many taxonomic units comprising the complex may be a consequence of these processes. One might suspect that the species and subspecies contain populations possessing distinctive habits or genetic make-up. This group, therefore, should present exceptionally fine opportunities for studies in speciation in mosquitoes, especially as the *Stegomyia* species adapt themselves rather readily to laboratory conditions. However, relatively few hybridization experiments have been conducted with them.

Woodhill (62, 63) observed that the cross between female *Aedes scutellaris scutellaris* (Walker) and male *Aedes scutellaris katherinensis* Woodhill was completely fertile, while the reciprocal cross was sterile. The progeny of the former cross were bred through three generations, and were entirely normal. The cross between these hybrid males and *katherinensis* females was sterile, while those between hybrid females and *katherinensis* males, and between the hybrids and *scutellaris* in both directions, were fertile. Crosses between *Aedes pseudoscutellaris* (Theobald) and *scutellaris* or *katherinensis* were sterile. The author concluded that *katherinensis* and *scutellaris* are subspecies. The complete sterility barrier leaves little doubt that both are specifically distinct from *pseudoscutellaris*.

These experiments were extended by Smith-White & Woodhill (53) to include a number of backcrosses between the *scutellaris* female×*katherinensis* male hybrids. The backcross females were fertile with *katherinensis* males through six generations of backcrossing; however, the reciprocal cross, *katherinensis* females×backcross males produced no viable offspring.

A. scutellaris scutellaris and *Aedes pernotatus* Farner & Bohart in Espiritu Santo, New Hebrides, were crossed experimentally by Perry (43). Only three of 18 hybrid F_1 females produced viable eggs after backcrossing with *pernotatus* males, and only one female and four males could be reared from the 96 larvae which hatched. The genetic barrier, combined with biological differences, leaves little doubt that *pernotatus* is specifically distinct from *scutellaris*.

Aedes polynesiensis Marks, formerly confused with *A. pseudoscutellaris*, has a wide distribution in Oceania. True *pseudoscutellaris* is restricted to Fiji [Marks (36)]. Woodhill (64), using *polynesiensis* from Tahiti, and *pseudoscutellaris* from Fiji, obtained greatly reduced percentages of hybrid eggs which hatched, but the progeny were normal and were bred through to the F_2 generation. Rozeboom & Gilford (51) carried out a similar study with *pseudoscutellaris* from Fiji and *polynesiensis* from Samoa. No difficulty was experienced in establishing hybrid colonies from crosses in both directions. The cross-fertilized female parent produced as many eggs as did the controls. There was, however, a difference in the fertility of the hybrid eggs. From 60 to 87.2 per cent of the eggs were fertile in the *pseudoscutellaris* and *polynesiensis* controls, but only 8.0 to 31.2 per cent of the F_1 hybrid eggs were fertile. In the F_2 and F_3 generations the fertility of the hybrid eggs was comparable to that of the controls. Thus a partial barrier appears to exist in the reduced fertility of the F_1 eggs. Laven and Dobrotworsky found that nonvi-

able embryos were present in the unsuccessful *molestus* and *pipiens* crosses. B. N. Gilford (unpublished results) dissected a number of eggs of the *pseudoscutellaris*×*polynesiensis* cross, and found that for the most part, the sterile eggs showed no evidence of embryological development. The barrier, therefore, is in the lack of cross insemination and possibly the inability of sperm to fertilize the eggs. Mating selection experiments also demonstrated the importance of the mating barrier. In view of the closeness of their results, it is not surprising that Woodhill, and Rozeboom & Gilford, arrived at a similar conclusion, i.e., that *polynesiensis* and *pseudoscutellaris* can not be considered to be true species unless other barriers can be demonstrated in Fiji, where the two coexist.

Inter- and Intraspecific Crosses of Other Stegomyias

Several authors have reported more or less successful hybridization of *Aedes aegypti* (Linnaeus) and *Aedes albopictus* (Skuse). These results are of interest not because they suggest the possibility of the establishment of hybrid populations in nature, but because of the peculiar inheritance of morphological characters. There have been no recent publications on this subject, and the earlier papers have been reviewed by Kitzmiller (25) and Mattingly (41). Rozeboom has recently attempted the *albopictus*×*aegypti* cross under conditions which precluded the possibility of insemination through the screen of the cage of experimental females by loose males. Of several hundred eggs obtained, not one hatched. Rozeboom & Gilford (51) obtained no viable eggs in a hybridization experiment between *polynesiensis* and *aegypti*.

Summers-Connal (55) and Mattingly (40, 41) have pointed out the existence of dark and pale strains of *A. aegypti*. In most places, this species is notoriously a close associate of man, living throughout most of its range exclusively in the domestic environment. However, in its original home, which presumably is Africa, populations have been observed which appear to be quite independent of man. In Kenya, Teesdale (56) placed bamboo pots as egg traps in various locations, and found that the females would oviposit 72 feet above ground, and that they would feed 50 feet above ground. Both males and females entered unoccupied as well as occupied dwellings, and females attacked out-of-doors, especially in the latter part of the day. Thus they appeared to enter houses for shelter, and not especially to feed. Furthermore, precipitin tests indicated the presence of an important, but unidentified, host other than man and domestic animals.

Gillett (21) has made a comparative study of two strains of *A. aegypti*, one from an isolated dry plateau of Tanganyika, and the other from a high rainfall area in Nigeria. The eggs of the Tanganyika strain responded readily to a hatching stimulus, while those from Nigeria were refractory. This response was shown to be an inherited character, and it was concluded that both males and females influenced the hatching behavior of the eggs. Hybrid eggs resembled those of the Tanganyika strain. Another inherited difference was shown to exist in ovulation and oviposition [Gillett (22)]. These, and

other differences, point to the existence of strains divergent in habits and physiology so as to be better adapted to their environments, and with these differences under genetic control.

Hybridization among *Anopheles* Species

The earlier work on hybridization among species of *Anopheles* has been reviewed by Kitzmiller (25) and so will not be reconsidered in detail here. Although some success has been reported in obtaining viable eggs from crosses between distinct species, for the most part the barriers between species have been found to be quite severe. In North America, *Anopheles quadrimaculatus* Say, *Anopheles freeborni* Aitkin, and *Anopheles azetecus* Hoffmann are separated not only geographically, but also genetically and by mating barriers. Burgess (5) obtained some fertile eggs in *A. quadrimaculatus* ×*freeborni* crosses, but none of the larvae attained the fourth stage. Barr (1) obtained 13 and 16 per cent hatching of several thousand eggs from his *quadrimaculatus*×*freeborni* crosses; most of the larvae died in the first instar, two pupated, and one adult male was produced, which was shown to be fertile by backcrossing with *freeborni* females. In several *quadrimaculatus* ×*aztecus* crosses, from zero to 57 per cent of several thousand eggs hatched, but none of the larvae developed beyond the third stage. In five *aztecus* ×*freeborni* crosses, many thousands of eggs were produced, with fertility ranging from 20 to 81 per cent. Many of the larvae were able to pupate, and a number of adults were obtained, which, though weak, were shown to be fertile by backcrossing and interbreeding. Thus *aztecus* and *freeborni* show a closer relationship to one another than to *quadrimaculatus*. The position of other two members of this group, *Anopheles occidentalis* Dyar & Knab and *Anopheles earlei* Vargas, have not as yet been determined. They are generally accepted as species, but in all probability they are closely related to one another and to *freeborni*, and observations in the laboratory and in nature on hybridization should be of great interest.

Two other interspecific hybridizations merit notice. Maryon, Lee & Shute (39) were able to hybridize *Anopheles labranchiae atroparvus* Thiel and *A. quadrimaculatus;* while Burgess (6) was even able to obtain viable eggs from crosses between *Anopheles punctipennis* (Say) and *quadrimaculatus*. In all of these *Anopheles* crosses, no completely successful hybridization between species was possible. It would appear unlikely that the few fertile but weakened adults such as those produced in Barr's experiments would be capable of establishing a hybrid progeny. This seems even more unlikely in view of the mating barriers which exist between the Nearctic species [Rozeboom (49)]. These experiments with *Anopheles* demonstrate the types of barriers one may expect to encounter between species, regardless of their morphological similarity or dissimilarity. Such results are in marked contrast to those observed between populations of the same species, even though they may have been geographically separated for long periods of time.

In South America cytogenetic studies, similar to those of Frizzi (14, 15),

are under way on the species of the subgenus *Nyssorhynchus*. These species are closely related and contain morphologically and biologically dissimilar populations. Aberrant forms such as *Anopheles rondoni* (Neiva and Pinto), *Anopheles triannulatus* Neiva and Pinto, *Anopheles bisignatus* Hoffman, etc., are strikingly different from the typical populations of their respective species. In a preliminary report, Frizzi & Ricciardi (16) have presented a map of the salivary chromosomes of *Anopheles aquasalis* Curry. The mitotic picture in the cephalic ganglia of *aquasalis* shows three pairs of metacentric chromosomes; whereas in *Anopheles albimanus* Wiedemann there are two pairs of metacentric and one pair of rod-shaped chromosomes. The authors anticipate the detection of intraspecific relationships through cytological comparisons. The South American anophelines should present an excellent field for such work. Opportunity for extensive work on anophelines is made evident by the taxonomic literature, which contains many references to "varieties" and "races" based on morphological characters. Such morphological comparisons, plus cytological studies, establish the existence of different populations. The affinities between such populations should be tested finally through hybridization experiments.

Discussion

Practical taxonomy will always utilize morphological criteria for separation of most species, but many systematists, when confronted with groups of closely related species or subspecies, have attempted to interpret the status of such populations in accordance with recently developed concepts of the species and its subdivisions. Populations separated by genetic or other barriers which would restrict gene flow are considered to be specifically distinct; populations differing from one another by some morphological or biological character, but capable of hybridization, are recognized as subspecies.

The problem of *molestus* populations and their place in the taxonomic picture is an extremely complicated one. *Molestus* is morphologically similar to *pipiens*, but very dissimilar physiologically; both *pipiens* and *fatigans* seem to be further removed physiologically from *molestus* than they are from one another. Some populations of *molestus* will interbreed with *pipiens* or *fatigans* or both, but widespread sterility exists among different populations of *molestus*. One might argue that the *molestus* phenotype actually represents a fairly common recombination of genes, already present in *pipiens* populations. This combination of genes might then be selected by a specific type of environmental situation, producing *molestus*. This argues of course for the widespread distribution of "*molestus*" genes throughout the *pipiens* populations. In modern genetic terminology "*molestus*" would represent isolated populations in which the frequencies of certain genes were much different than in the normal *pipiens* population. Continued isolation and presumably selective advantage of the "biotype" might eventually permit the accumulation of cytoplasmic differences, which in turn take over as isolating mecha-

nisms. If this be the case, we are dealing with an unusual and interesting type of mechanism of speciation.

In interpreting the peculiar inheritance of the interspecific crosses between *Stegomyia* species, in which the progeny resembled the female parent, Toumanoff (57) rejected the hypotheses of a selective mortality of the embryos or larvae, and of parthenogenetic development of the eggs. He concluded that the phenomenon was explainable on the basis of cytoplasmic inheritance. However, Mattingly (41) argues that the appearance of an *aegypti*-like "throwback" in the F_4 generation of Toumanoff's *albopictus* ♀ × *aegypti* ♂ crosses required an explanation other than cytoplasmic inheritance, in that a character, originating in the paternal chromosomes, survived through four generations.

Smith-White & Woodhill (53), who showed that a nonreciprocal sterility existed between *Aedes scutellaris scutellaris* and *A. s. katherinensis*, concluded that the phenomenon could be explained either on the basis of cytoplasmic inheritance or "uniparental inheritance of cytoplasm-conditioning genes." In the latter hypothesis a cytoplasm-conditioning gene from *katherinensis*, carried on polarized chromatin, would modify the cytoplasm from *scutellaris* from a neutral to a *katherinensis* condition. The allele of this gene must be dominant, and both must be inherited on chromosome segments derived from the mother. It is pointed out that there is no cytological or genetical evidence for these assumptions, but that if rejected, "an explanation based on cytoplasmic inheritance independent of the genotype must be invoked."

Laven (31) agrees that the phenomenon of maternal inheritance which he observed in his *Culex* crosses can be explained only by the two hypotheses advanced by Smith-White and Woodhill. However, he notes that with the present availability of x-ray induced mutant genes as markers, it is possible to obtain evidence as to which of the hypotheses is correct. The two autosomes and the male and female sex chromosomes can be marked with four of the mutant genes. These display definite Mendelian ratios in the F_2, and on outcrossing to other populations, there is no evidence of polarized segregation. Thus the cytoplasmic hypothesis is the most logical. Further evidence is seen in repeated backcrossing of hybrid females of Hamburg × Oggelshausen cross to Oggelshausen males, which should result in replacement of the H genome by O. Yet, after 60 serial backcrosses, the hybrid males were still intersterile with Oggelshausen females. Thus, a character within the cytoplasm, independent of the nucleus, has remained unchanged.

Although cytoplasmic inheritance has been described for plants and certain animals, its presence in at least two and possibly additional groups of mosquitoes would indicate that extensive studies on mosquito genetics may uncover other phenomena which will contribute to genetic and evolutionary theory. One may wonder what correlations may exist between structural chromosomal rearrangements and populations which differ morphologically and biologically from one another. But aside from these more purely biological considerations, most entomologists, because of their interests and train-

ing, would ask the question as to what application there may be to present day problems involving insects and man.

To date, even the limited studies on speciation and genetics of mosquitoes have shown that considerable variability exists in species. Population dynamics have a real application to public health. It has been the business of the medical entomologist to discover and control disease-bearing arthropods. This involved taxonomic studies so that the dangerous species could be separated from harmless relatives, the determinations of experimental and natural infection indices as proof of vector role, and ecologic observations to reveal the niche occupied by the vector species. The availability of the new, powerful insecticides has made it unnecessary in many cases to carry out the preliminary investigations and surveys prior to the application of practical control measures against disease vectors. There remain, however, certain special problems in medical entomology. There are residual foci of disease, in which the mechanisms of survival are obscure. Two examples are yellow fever and perhaps dengue in rural areas. Such foci are of importance for two reasons: within their boundaries sporadic cases occur among rural peoples, and these foci remain as a source of potential danger of epidemics in more densely settled areas. Although we possess the means of curbing such epidemics, the need for vigilance and maintenance of protective measures is expensive. The survival of diseases in such foci are interesting biological phenomena, which may have to do with population dynamics involving the same processes which lead to speciation. Thus Bugher (4) commenting upon the recent extension of yellow fever through Central America says:

> In the whole epidemiological complex one of the most significant things seems to be the essential fluidity of living things, both vectors and host. In the biological complex we tend to think too much in taxonomic terms and perhaps do not fully appreciate that within what is called a species, which is quite an arbitrary thing anyway, there is not only variation geographically but there is variation in time within the same geographic area. So the biological behavior of a species unit, whether a mammal—that is, a monkey—or a mosquito, may vary from area to area at the same time and within a given area at different times.

Following the application of wide scale unrestricted control measures against mosquitoes, especially for malaria eradication, some species have been undergoing intensive selection pressure which may well accelerate the changes occurring within a given area. This is true particularly of the domestic species which have been forced to live in close contact with residual DDT. Whether such evolutionary pressures will lead to the formation of disease-bearing populations which will attack man out-of-doors, remains to be seen. We have evidence that there are residual, wild-type populations within highly domestic species, and that changes in habits have been occurring among other domestic and semidomestic species. Two examples are *Anopheles darlingi* Root in Brazil [Bustamante (7)], and *A. albimanus* in Panama [Trapido (58)]. A more recent observation is that of Ferreira & Azambuja (12) on species of the *Anopheles* subgenus *Kerteszia* in the south littoral area of

Brazil. In this area, these mosquitoes are malaria vectors and residual DDT applied inside houses was an effective control. In 1954 there was an increase in autochthonous cases of malaria in certain localities. It was found that the mosquitoes were resting on the outside rather than on the inside of houses. That this represented a modified resting habit was indicated by the fact that in another area where DDT had never been used, most of the resting adults were taken inside houses.

In summary, the evolutionary mechanisms leading to speciation in mosquitoes are of interest because they may contribute to basic biologic knowledge and theory; they appear to be involved in unexplained phenomena in the survival and epidemiology of disease; and eventually they may have to be taken into consideration in connection with control of diseases. One of the approaches to studies on speciation is through crossbreeding experiments with species or subspecific populations. The immediate results of such research may show whether the populations in question are of specific or subspecific status. There are, however, far broader implications than the immediate taxonomic objectives. Hybridization experiments will show to what extent the existing members of species complexes have diverged; this, combined with comparative studies on distribution, biology and ecology, should give us an insight as to the evolutionary dynamics which apply to the three basic interests referred to above.

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THE FEEDING HABITS OF BITING FLIES AND THEIR SIGNIFICANCE IN CLASSIFICATION[1,2]

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The object of this review is twofold: first, to examine the feeding habits of the biting flies belonging to the Nematocera and the first section (Homoeodactyla) of the Brachycera; and secondly, in the course of brief comparisons with other Diptera, to discuss some phylogenetic considerations.

The term *biting flies* applies to flies whose mouth parts are adapted to pierce the integument and suck the body fluids, whether of vertebrates or other animals. In the families under detailed review, the habit of biting, and fully functional biting mouthparts, are restricted to the females. Most frequently the females attack warm-blooded vertebrates, and an immense literature has grown around this habit and its medical implications. In this review, however, the lesser-known sources of the blood meal are stressed, in an attempt to define the full range of the habits. Both sexes, in addition, take a meal of sugar and water, usually the nectar of flowers. Many authors, however, have considered sugar feeding (or, as it is often vaguely expressed, "sucking the juices of plants") as typical of the males, and have treated it, in the females, as a "supplementary" habit, an occasional phenomenon induced by adverse conditions, or even as an error of observation. Thus, in varying degrees, an unreal opposition between carnivorous females and vegetarian males is set up. The nectar-sucking habit, however, is fully established for both sexes; and nectar-sucking and blood-sucking are habits each of its own kind.

Culicidae

Mouth parts.—The mouth parts of mosquitoes are very slender and the female, when biting, commonly penetrates a capillary vessel, a delicate process that is probably not possible with the more bladelike organs of other families. The mandible is armed at the apex with a row of minute teeth, and the lacinia [Imms (1)] bears coarser, backwardly projecting teeth, probably with a holding function [Robinson (2)]. The equally elongate labrum and hypopharynx are apposed to form a food canal, and liquid is drawn up by two pumps, one operated by the cibarial and the other by the postcerebral pharyngeal muscles. Mouthparts of the same general structure, with similar armature of the mandibles and laciniae, are found throughout the biting Nematocera [Snodgrass (3)]. In the males the mandibles and maxillae are reduced, to varying degrees, to a nonfunctional condition [Marshall & Staley

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[2] The survey of literature pertaining to this review was completed in June, 1957.

(4)]; the food canal, however, remains intact. No reports of biting by males, in Culicidae or other Nematocera, have been substantiated; the males of a few species land on the host of the female to drink sweat or to mate [Howard, Dyar & Knab (5); Downes (6)], but other apparent males proved to be gynandromorphs, with female elements in the sense organs (7).

Food sources.—The females of most mosquitoes obtain their blood meals from warm-blooded vertebrates. Mammals and birds are both freely attacked, and although some species are relatively restricted others have a wide range of hosts in both classes. A few feed on amphibia and, perhaps, on reptiles. *Culex* (*Neoculex*) *apicalis* Adams and several other species of the subgenus feed only on frogs and toads, some earlier records from mammals notwithstanding (8, 9). *Uranotaenia lowii* Theobald feeds on amphibia (10) and unidentified mosquitoes are said to attack terrapins and lizards (5). In captivity both *Aedes aegypti* (Linnaeus) and *Culex pipiens* Linnaeus will feed on reptiles (11).

There are several records of more curious habits but none that indicate that female mosquitoes take their specific meal from any source other than the blood of vertebrates. Howard *et al.* (5) quoted accounts of mosquitoes feeding on cicadas, dead chironomids, and the pupae of butterflies, but the first two remain unconfirmed and are probably accidental and the last is a misquotation from Hagen (12). Reports of females feeding on plants, except from the nectaries, seem to be of equally doubtful significance (13). In many mosquitoes blood-sucking is unknown; frequently, perhaps, their habits merely await discovery, but in *Toxorhynchites* and *Harpagomyia* the proboscis is modified and unsuited for biting [Edwards (14)]. In the related groups, Chaoborinae and Dixidae, blood-sucking is also unknown, although mandibles and maxillae are present in a reduced form (14), as they are in the pupa, but not the adult, of *Harpagomyia* (15).

In addition to the blood meal of the female, mosquitoes take in sugar-rich substances, typically without piercing. The reports on sugar-feeding in nature are scattered. Knab (16), in a review, showed that both sexes of species of *Culex* and *Aedes* frequently visited flowers for nectar. Wesenberg-Lund (17) found *Aedes* spp. probing at dandelions, but he believed it was an exceptional occurrence due to unfavorable weather that prevented the search for a blood meal. Hocking (18) assembled another group of records of nectar-sucking, relating to six genera and including many biting species, and treated them as so many cases of a general phenomenon (Hocking's lists, of Culicidae and of other families, omit several references to males that occur in the original reports).

Principally as a result of studies at Churchill, Manitoba, many Canadian entomologists are aware that *Aedes* spp., and also black flies and tabanids, feed on nectar regularly and in very large numbers. The published information is not extensive, but it includes records of females of *Aedes punctor* (Kirby) on *Habenaria*, of undetermined species on *Rhododendron*, *Dryas*, *Habenaria* and *Ledum*, and of both sexes of *Aedes communis* (De Geer) on a

variety of flowers (18). From my own observations both sexes of *A. communis*, *Aedes hexodontus* Dyar and *Aedes nigripes* (Zetterstedt) also visit *Rubus*, *Salix*, *Epilobium*, *Cicuta* and *Heracleum*, the males predominating in the afternoon and the females late in the evening. In contrast, however, to the situation at Churchill, mosquitoes were found on flowers in southern Quebec only singly and at long intervals.

Some species of *Anopheles* can, perhaps, dispense with the sugar meal (see below), but it is unlikely that this is generally the case. Denisova (19) reported that glucose is found "frequently" in the crop of *Anopheles maculipennis* Meigen; Haeger (20) found *Anopheles atropos* Dyar and Knab on honeydew; Munroe (*in litt.*) has seen overwintered females at the moth-collector's "sugar," and Hocking (18) has quoted two records from flowers.

In spite of these and similar records, little is known of the sources of sugar and the mosquitoes that frequent them, of sexual differences, of rhythms of feeding or of effects of climate or weather. The northern species are common on the flowers of Compositae, Rosaceae, and *Salix*, but the degree of specificity is unknown. Other possible sources of sugar, such as wounded trees, honeydew, extrafloral nectaries, and the secretions of rust fungi, remain unexplored except for a few observations by Haeger (20). There is a small group of observations on the time of the sugar meal in relation to other activities [Larsen (21); Nielsen and Greve (22); Hocking (18); Haeger (20)] but only limited conclusions can be drawn.

The remarkable habits of *Harpagomyia* spp. remain to be considered. These mosquitoes haunt the foraging trails of ants and solicit food; the ant stops, opens its mouth parts and regurgitates liquid, which the mosquito imbibes [Jacobson (23); Farquharson (24)]. Poulton (see 25) showed conclusively that the habit was common to both sexes, a suggestion that had caused considerable surprise when first made. However, Jacobson had already recorded that the ants were foraging among colonies of coccids, i.e., they were collecting honeydew; and he had also found that dyed honey, fed to ants, was rapidly distributed to the mosquitoes. The mosquitoes, therefore, were obtaining a sugar meal, not a peculiar analogue of the blood meal; and the process is extraordinary only from the behavioral, and not from the dietary, point of view.

Utilization of the food.—The females of blood-sucking mosquitoes need blood for the development of the oocytes [Wigglesworth (26); Bates (27)]. In *Anopheles elutus* Edwards and *Aedes hexodontus* the oocytes develop slightly (to stage II) before the blood meal (28, 29), but in *Anopheles gambiae* Giles the first of the two blood meals brings the oocytes to stage II, and the second to maturity (30). Most species complete the gonotrophic cycle on a single meal, but *Anopheles maculipennis* (*sens. lat.*) may need several meals, especially towards hibernation, and old individuals of *Aedes* spp. take a succession, without ovarian development resulting (31). In some species fertilization is a necessary precursor to development.

A few mosquitoes, commonly members of otherwise normal genera, lay

one batch of eggs without a blood meal, by drawing on reserves accumulated during larval life. They must then feed as usual to begin the second cycle. The "autogenous" race of *Culex pipiens* emerges with reserve fat and protein in the fat-body [de Boisseson (32)]. In a strain of *Aedes communis* that probably dies without biting, after one oviposition, the ovaries mature at the expense of the autolyzing wing muscles (33) or of the fat body and larval muscles (29). Clements (34) has suggested, however, that in some cases hormonal control rather than lack of reserves is the decisive factor in inhibiting maturation before the blood meal; in *C. pipiens* the reserves differ only slightly between the autogenous and anautogenous forms.

Alone among the biting Nematocera, certain mosquitoes hibernate as adults. Some species of *Anopheles* lay down reserves in the fat body during the last ovarian cycles of summer and then become dormant; others cease oviposition but continue to bite throughout the winter [Bates (27)]. The transition from normal cycles to this condition of "gonotrophic dissociation" is not sharp; and during both the cessation of ovarian development and its reestablishment in the spring, a resorption of oocytes occurs (35, 36), much as in *Rhodnius* after removal of the corpora allata. Both these and the more direct observations of Detinova (37) again indicate hormonal activity. The winter reserves of *Anopheles* apparently consist of fat. Bettini (38) detected no stored protein; and a blood meal is necessary before the first oviposition of spring (35, 36). The fat is almost certainly elaborated largely from blood meals, although Hecht (39) noted that sugar may serve as a supplement. *Anopheles occidentalis* Dyar and Knab, by exception, hibernates without a blood meal, under severe northern conditions in which it becomes immobilized and rigid (40, 41).

In culicines the preparation for hibernation is different. *Culex pipiens* does not bite, but lays down fat in the fat body as a result of sugar feeding; a blood meal is again required in the spring [Buxton (42); Tate & Vincent (43)]. *Culiseta impatiens* (Walker) mates and feeds on sugar in summer and then becomes dormant until spring, when it bites and oviposits [Frohne (40)]. It seems, therefore, that at least three types of storage of reserves must be distinguished. Autogenous species emerge with stores of glycogen, fat and protein in various tissues. Hibernating species probably store fat only, mainly in the fat body; but whereas the fat is derived from blood in *Anopheles*, in culicines it is metabolized from carbohydrate.

The sugar meal of mosquitoes, and, initially, the reserve glycogen, yields energy for flight [Hocking (18)]. It is necessary also for normal longevity in both sexes, and is always provided for laboratory colonies. Blood-fed females of *Anopheles atroparvus* van Thiel survive for a maximum of 14 days without sugar (44), as against six weeks in nature. Many species can survive without sugar to complete the first ovarian cycle, but *Aedes hexodontus* dies before oviposition (45). Some species, however, can obtain energy from the blood meal. Thomson (46) found that *Anopheles gambiae* lived for 86 days on 30 blood meals but without other food, and in hibernation also *Anopheles* spp.

utilize blood alone; but Thomson's opinion that the sugar meal is generally unnecessary is evidently without foundation. Clements (47) showed that *Culex pipiens* can use a part of the blood meal (more than its content of sugar) for flight.

Simuliidae

The mandibles and laciniae are well-developed bladelike organs in the females of most black flies, but in *Cnephia dacotensis* (Dyar & Shannon) and in several other species they are reduced and nonfunctional [Nicholson (48); Rubtzov (49); Davies & Peterson (50)]. The females attack warm-blooded vertebrates; and although most records refer to mammals, feeding on birds is not uncommon (50). *Simulium arcticum* Malloch feeds mainly on cattle (51) and *Simulium rugglesi* Nicholson and Mickel on birds (52), but others such as *Simulium griseicolle* Becker, have a wide range of hosts including both birds and mammals (53). There are no records from reptiles and amphibia and the evidence that black flies attack insects is slight. Pryer (54) found a "minute yellow *Simulium*" feeding on a moth, and Hagen (12) saw black flies on the pupae of butterflies; but it has been suggested, almost certainly correctly in the first case, that the predators were ceratopogonids. Hill (55) mentioned an insectivorous species in Australia, but it does not appear in subsequent reviews; and Peterson (56) found a female *Simulium vittatum* Zetterstedt feeding on an ant. Howard *et al.* (5) noted reports of black flies attacking young fish, but the original accounts seem to point to some other insect.

Most species are believed to need a blood meal for ovarian development and this has been confirmed by experiment in several cases (e.g., 51, 57). Lewis (58) found, in *Simulium damnosum* Theobald, that the blood meal initiated development of the accessory glands as well as of the ovaries; Wanson & Lebied (59) showed that this species can complete three gonotrophic cycles. If the blood meal is insufficient the development of all the oocytes is interrupted (60) but in *Prosimulium hirtipes* (Fries) some oocytes can mature while others remain small (57). On the other hand, *S. vittatum* and *P. hirtipes*, in Michigan, develop mature ovaries when maintained on sugar and water only, although both species bite elsewhere (57). The species with reduced mouth parts emerge with the oocytes either almost ripe or only partially developed and with a large fat body; the condition of the eggs and fat body also varies among those with normal mouthparts (50, 61). *C. dacotensis* takes neither blood nor sugar (6).

Both sexes of many species have been found on flowers and other natural sources of sugar [Hocking (18); Bequaert (62)] and the records include the females of important blood-sucking forms. Lewis (53, 58) found both sexes of *S. griseicolle* on date flowers and at fallen mangoes, and plant sugars in the crop of *S. damnosum*; a few pollen grains may also be ingested, apparently by accident. Davies & Peterson (50) found nectar in the crop regularly and suggested that *Vaccinium* was the important source. Davies (63) showed that

females of *Simulium venustum* Say need sugar for normal longevity and also that survival on a diet of sugar and blood was about the same as on sugar alone, which suggests that the blood meal does not contribute significantly. Rubtzov (60) concluded that four European species need not only blood but also water and sugar in order to complete the first ovarian cycle.

Ceratopogonidae (Heleidae)

The biting midges are remarkable for great diversity of sources of the blood meal or its analogue. The family comprises four subfamilies: the Leptoconopinae (monotypic); the Forcipomyiinae with *Atrichopogon* and *Forcipomyia* and its allies; the Dasyheleinae (monotypic); and the Ceratopogoninae (Heleinae). The Ceratopogoninae comprise the Culicoidini (monotypic) and three other tribes, each with several genera. This classification is frequently, but not rigidly, reflected in the feeding habits. *Leptoconops* is perhaps closer to *Culicoides* than is commonly supposed.

The females of *Culicoides*, *Leptoconops* and *Lasiohelea* attack vertebrate hosts. Several species of *Lasiohelea*, an ill-defined genus near *Forcipomyia*, attack mammals [Tokunaga (64); Mayer (65)], and *Lasiohelea velox* (Winnertz) feeds on frogs [Desportes (8)]. *Leptoconops* spp. feed on mammals and birds and have a reputation as vicious biters [Noè (66); Mayer (65)]. Many species of *Culicoides* feed on mammals and an increasing number have been recorded from birds [Painter (67); Tokunaga (68); Snow *et al.* (69); Downes (70)]. In addition, *Culicoides piliferus* Root and Hoffman has been taken on the turtle *Clemys insculpta* in Pennsylvania (Wirth, *in litt.*) and Myers (71) indicates that *C. furens* (Poey) will attack lizards; but the statment that *Culicoides oxystoma* Kieffer feeds on earthworms is incorrect. *Culicoides anophelis* Edwards obtains a meal of mammalian blood by piercing the abdomen of recently engorged mosquitoes [Edwards (72)], but it also feeds directly from cattle [Smith & Swaminath (73)] and this is doubtless the primary habit.

In the Forcipomyiinae, except for *Lasiohelea* and a very few other species, the females attack larger insects without, apparently, doing serious injury. *Forcipomyia* spp. are found on sawfly and lepidopterous larvae, phasmids, tipulids, culicids, and opilionids (Arachnida) and one group feeds through the wing veins of Neuroptera, Lepidoptera, or Odonata. The related genus *Pterobosca* similarly attacks the wings of Odonata [Wirth (74)]. *Forcipomyia eques* (Johannsen) remains on the wing of *Chrysopa* sp. for three days, while blood is slowly imbibed and the oocytes mature (personal observation), and the brachypterous species *Forcipomyia ixodoides* (Fiebrig-Gertz) similarly remains attached to a phasmid (75). This gradual method of feeding is probably common, and the midges have often been found on museum specimens of the host.

In *Atrichopogon*, the species of the subgenus *Meloehelea* attack oil beetles [Wirth (76)]. Vogel (77) found a species on the wing of a moth, as in *Forcipomyia*, and Edwards (78) another on mealy bugs, but two records on mam-

mals (65) seem to need confirmation. The very exceptional species *Atrichopogon pollinivorus* Downes, which is associated with the flowers of honeysuckle, obtains the blood meal analogue from the pollen grains [Downes (13)]. There is no other well-established case, among the Nematocera, of the female obtaining her specific food from a plant source, but in *Forcipomyia quasiingrami* Macfie the females, alone, enter the flowers of cacao (79), perhaps for a similar reason.

In the Ceratopogoninae, *Culicoides* excepted, the females catch small insects of about their own size in flight, and the prey is killed as the body fluids are sucked out. In most cases the prey consists of Chironomidae (Tendipedidae) and other Ceratopogonidae, usually males, or small Ephemeroptera (80 to 83 and personal observations), but *Palpomyia* sp. has been found on a stone-fly. The midges usually attack their prey in one of the localized male swarms that are so characteristic of many species of these groups. The females of several species, in addition to their other prey, eat the male during copulation and may carry the male terminalia still attached in the copulatory position after the remainder of the empty cuticle has broken away [Goetghebuer (84); Edwards (80)]. Some of these species themselves produce male swarms, which the female enters at mating time; this suggests that the mating behavior and the feeding behavior have converged.

A blood meal is necessary for ovarian development in *Culicoides* spp. [Hill (85); Nicholas (86)], in *Leptoconops* spp. [Smith & Lowe (87)], and in the frog-biting species *Lasiohelea velox*. Presumably this is so among the insectivorous forms also, none of which have been tested. In *Culicoides nubeculosus* (Meigen) one blood meal is usually sufficient for maturation, and as many as five cycles can occur [Downes (88); Megahed (89)].

Again, however, a number of autogenous species are known. *Culicoides gigas* Root and Hoffman completes the first ovarian cycle without a meal and then feeds; and several other species, one of them with reduced mouth parts, are nonbiting (70). Gad (90) found species with reduced mouth parts in *Forcipomyia* and *Dasyhelea*, and ovarian develpment occurs spontaneously in several species of the latter genus, which may consist wholly of nonbiting forms (13).

The mouth parts of the Ceratopogonidae vary slightly according to the nature of the food [Gad (90)]. In the Forcipomyiinae the teeth of the laciniae of some of the insectivorous species are of an unusual type, presumably in relation to the holding of rigid cuticle (91). In the insectivorous Ceratopogoninae the mandibles are broad blades with unusually large teeth, but the laciniae, though still present, are reduced. All parts are present in the male, but the armature is reduced.

Males and females of many species in each of the chief groups visit flowers for nectar. Mayer (92) has collected some earlier records, and others are scattered through Kieffer's taxonomic works. Both sexes of *Culicoides* sp. abound on *Heracleum* and *Cicuta* shortly before the peak of the flight period, but several other species at the same site were never found on flowers (70).

Both sexes of *Leptoconops irritans* (Noè) and *Leptoconops bezzii* (Noè), the chief pest species in Italy, feed on the flowers of *Euonymus* (66). Kieffer (93) has also reported that the females (only) of two species of *Culicoides* are attracted to the inflorescence of *Arum*. This, however, is probably a special case in which the attraction of the warm and odorous inflorescence is confused with that of a vertebrate host or, perhaps, is without biological significance.

In the Forcipomyiinae, two insectivorous species and many others, unidentified or not proved blood-suckers, have been found on flowers. At Churchill, many species of *Forcipomyia*, *Atrichopogon*, and also of *Dasyhelea* are found on *Cicuta*, *Heracleum*, *Ledum*, *Epilobium* and *Rorippa* and other plants. Both sexes of *Atrichopogon pollinivorus* feed on nectar, from the same flowers from which the females obtain the meal of pollen-sap. This species, therefore, exhibits the same duality as the blood-sucking forms; it is exceptional only as regards the source of the female-specific food [Downes (13)].

Among the insectivorous Ceratopogoninae some species visit flowers regularly, but for none of them is the prey also known. Kieffer (94) records the females of *Ceratopogon communis* Meigen from Umbelliferae, and both sexes of other species visit a variety of flowers at Churchill. *Schizohelea leucopeza* (Meigen) also frequents flowers, as usual collecting nectar; but curiously only females are sometimes so observed (90). Outside these two genera, records are so scarce as to raise the possibility that some species, at least, do not take a sugar meal and that the females satisfies all her needs on insect prey.

It is standard practice to provide colonies of *Culicoides* spp. with fruit or sugar, but little is known of their requirements. *Culicoides nubeculosus* drinks water and sugar solutions from the day of emergence onwards, whether or not the females have been blood-fed; but it can survive until oviposition without sugar (89 and personal observations).

Psychodidae

It is commonly supposed that *Phlebotomus* is the only bloodsucking genus in the Psychodidae, but two related genera have recently been discovered and biting forms occur also in other sections of the family [Fairchild (95)]. *Horaiella* has well-developed, toothed mandibles and reduced maxillae (cf. Ceratopogoninae), but its food is unknown [Tonnoir (96)]; and *Sycorax*, a genus now represented by a few widely scattered species, feeds on frogs [Desportes (8)]. These two genera are of uncertain systematic position and are variously placed by Tonnoir, Theodor (97), Hennig (98) and Fairchild (95). The Psychodidae therefore include either two or three main stocks with biting mouth parts; and it is likely that biting mouth parts, although absent in one large group (Psychodinae) and in two primitive genera, are a basic family characteristic.

Phlebotomus has a wide range of vertebrate hosts and many of the species attack reptiles. Thus, for example, *Phlebotomus schwetzi* Adler, Theodor and

Parrot feeds on man, monkeys, rabbits, bats, fowl and lizards (99). *Phlebotomus noguchii* Shannon, on the other hand, seems almost confined to field mice (100). Kirk & Lewis (99) believe that some desert species have no adequate supply of vertebrate hosts, and suggest some other source of food. Experimentally, a blood meal has been found necessary for ovarian development (100, 101, 102). Dolmatova (103) described the digestion of the blood and the concurrent development of the oocytes and lubricating glands in *Phlebotomus papatasi* (Scopoli). A small blood meal leads to the development of a few follicles only; but unfertilized females can produce normal eggs. *Phlebotomus perniciosus* Newstead needs only one meal for ovarian development, but *P. papatasi* may take up to five, possibly in part as a source of water (101, 103).

P. papatasi can survive to the time of laying without carbohydrate [Unsworth & Gordon (102)]. The insects were kept under conditions simulating those in crevices or in the burrows of small animals. Such habitats, common in nature, probably provide suitable temperature and humidity and a supply of blood, for a minimum expenditure of energy. Nevertheless, both sexes of *P. papatasi* accept sugar in the laboratory (104); and Barretto (105) showed that females of other species, provided with sugar, could complete three gonotrophic cycles. Kirk & Lewis (99) found sugars of plant origin in the crop of *P. papatasi* but the natural sources are not known.

Blepharoceridae

Information on the food of the Blepharoceridae is scanty, but conforms to the familiar pattern. The females attack other insects and, like some Ceratopogoninae, catch their prey in flight. *Blepharocera tenuipes* (Walker) feeds on chironomids, *Hapalothrix lugubris* Loew on *Hilara*, and *Liponeura cinerascens* (Loew) on tipulids (106, 107). *Curupira torrentium* (Brauer) is said to attack mammals, but Edwards (108) points out that the statement is due to a misunderstanding. As in the insectivorous Ceratopogoninae, the maxillae are shorter than the proboscis and probably nonfunctional (106). In several genera there are species with fully developed mandibles and others with these organs entirely lost; in one of the latter, *Edwardsina nigra* Edwards, the female emerges from the pupa with the ovaries already ripe (108). Edwards' generalization that in all the biting flies the mandibles of the female are either fully developed or entirely lacking is, however, evidently incorrect.

Both sexes of *Apistomyia elegans* (Bigot) feed on the nectar of composites. Schnuse's original observation, discredited by Kellogg, was established beyond doubt by Hetschko (109). Reference should also be made to the work of Mannheims (110), which was not available for this review.

Tabanidae and Rhagionidae

The females of most horse flies attack the larger mammals, but the tropical forest-canopy species presumably feed mainly on monkeys or other small forms [Fairchild (111)]. A few species of *Tabanus* attack crocodiles,

lizards or turtles but none have been recorded from amphibia or, curiously, from birds [Leclercq (112)]. Most species are presumed to take a blood meal, but several species and genera, distributed in all subfamilies, are nonbiting; occasionally the mandibles are reduced or absent [Mackerras (113, 114)].

Both sexes of many forms, including numerous biting species of *Tabanus*, *Chrysops*, and *Pangonia*, feed at flowers or at wounded trees, ripe fruit, or honeydew [Leclercq (112); Hocking (18)]. Mackerras (113) says that some Pangoniinae feed only on blood, others only on nectar and others on both. Both sexes also drink free water, and Neave (115) notes that in Africa this occurs chiefly in the dry season and that the females do not bite until the onset of the rains. Some species dip the tip of the abdomen into water as they fly.

Sugars are necessary both as a source of energy and to sustain life for the normal duration. In species of *Tabanus*, *Chrysops* and *Haematopota* the development of the oocytes is dependent on the blood meal and one meal suffices for maturation; there may be as many as five gonotrophic cycles in *Tabanus autumnalis* Linnaeus [Olsufiev (116)].

The mouth parts of the Tabanidae, and similarly of the Rhagionidae, are essentially similar to those of the Nematocera and all the characteristic structures are present. They agree also in certain small but significant details such as the fine apical teeth on the mandibles and the backwardly directed teeth on the maxillary blade. They differ, however, in the reduced segmentation of the palpi, the great development of the labellae and the position of the pharyngeal pump, which is operated by precerebral muscles. In the male the several parts are somewhat reduced, and the mandibles, at least in some species, absent [Snodgrass (3); Bonhag (117); Hoyt (118)].

In the Rhagionidae, as in the Psychodidae, the blood-sucking habit is more widespread than is generally recognized. The females of *Symphoromyia* spp. attack man in North America (119), and *Suragina longipes* (Bellardi) and *Dasyomma* spp. feed on mammals in Mexico and Chile (120, 121). *Atrichops crassipes* (Meigen) feeds on frogs (8). The supposed blood-sucking habits of *Rhagio* spp., however, must be discredited, and in *Vermileo* also the adults do not bite (120, 122). Becher (123) and Hoyt (118) have shown that mandibles are lacking in the females of *Rhagio* and *Chrysopilus*, but are well developed in *Symphoromyia* and *Atherix*. The Australian genus *Spaniopsis*, not closely related to the foregoing, is a well-known pest of man, and Malloch (121) suggests that *Austroleptis* may also be a blood-sucker. It is commonly said that Rhagionidae also feed on insects; but the original records, if any, have not been discovered. Certain species of *Rhagio* and *Atherix* visit flowers and honeydew [Knuth (124); Zoebelein (125)].

Comparisons and Phylogenetic Considerations

The principal generalization concerning the feeding habits of these biting flies is that a basic duality exists. In most species, both sexes feed on sugar, typically in nectar; and the female (only) also feeds on a complex protein-

rich food, typically the body fluids of vertebrates or insects. These foods have different functions: to sustain life and activity and to provide material for maturation of the oocytes; the precise nutritional picture is, however, not clear and there may be some overlapping of function. In some species of *Anopheles*, and possibly in some other forms, the females may maintain themselves from repeated blood meals; certainly this is so in *Anopheles* during hibernation. Typically, however, both foods are essential; ovarian development is initiated only by a blood meal and sugar is required for normal longevity and in extreme cases, apparently, for survival to the time of the first oviposition. The two meals are taken in by imbibing of free liquids and by piercing, respectively; and they pass into different parts of the gut (126). Even in aberrant circumstances they are identifiable and distinct, as in the vegetarian species *Atrichopogon pollinivorus* which takes both meals from honeysuckle flowers, and in *Harpagomyia* spp., whose females provide for ovarian ripening from internal reserves though both sexes obtain sugar from ants that have collected honey dew from coccids.

These flies have the full complement of insectan mouth parts. Piercing is effected principally by the apically toothed mandibles, assisted by the maxillae and other organs; in those that catch insect prey in flight, however, the maxillae are reduced. The liquid, whether blood or sugar, is taken in through a tube formed primarily of the apposed, elongate labrum and hypopharynx. In the males the piercing organs are reduced, or occasionally absent.

In all families certain species provide for the first maturation of the ovaries from internal reserves; they may or may not subsequently feed and lay again; similarly the mouth parts may or may not be reduced. The loss of the blood-sucking habit, with varying degrees of structural reduction, also occurs in larger groups (*Harpagomyia, Dasyhelea, Rhagio;* Chaoborinae, Psychodinae, Scepsidinae). The nonbiting species or groups are irregularly scattered within normal, biting taxa, and may reasonably be regarded as secondary.

These generalizations hold for all the families considered, both Nematocera and Brachycera Homoeodactyla, and indicate a strong link between these groups. Some wider comparisons can now be made.

Nematocera and Homoeodactyla: nonbiting families.—Many families of the Nematocera and Homoeodactyla, and in the former large groups of families are entirely nonbiting. The short-lived forms presumably take no food; others, in both sexes, visit flowers or honeydew (e.g., certain Chironomidae, Bibionidae, Mycetophilidae, Tipulidae, Stratiomyidae, Coenomyidae) [Knuth (124); Zoebelein (125)]. It is difficult, however, to trace satisfactory records of more complex foods analogous to the blood meal of the female biting flies. Some Scatopsidae, for example, lick moist dung; but many of them also oviposit on dung and the significance of the habit is not clear. According to Knuth (124) some Stratiomyidae obtain both nectar and pollen at flowers, and Rapp (see 125) appears to have confirmed this observation. The mouth parts are always reduced; mandibles are lacking, except as ves-

tiges in the Dixidae and Pelecorhyncidae, which are closely related to biting families [Edwards (14); Mackerras and Fuller (127)]; and the lacinia, though often persisting, is shortened [Peterson (128)]. Both in habits and structure, therefore, these families are comparable to forms such as *Toxorhynchites* or *Rhagio* among the biting flies. The reason for the general lack of a female-specific food, obtainable from many exposed sources, is not clear.

Heterodactyla and Cyclorrhapha.—A remarkable difference is evident in these, the remaining groups of the Diptera. As before, some do not feed; and others, e.g., the Bombyliidae, are restricted to the meal of sugar. Wherever more elaborate feeding habits are found, the same basic duality occurs. The insectivorous Asilidae and Empidae also feed on nectar; many Syrphidae and Anthomyiidae visit flowers for both nectar and pollen; *Hippelates* spp. feed on nectar and at open wounds; and *Musca domestica* Linnaeus, *Stomoxys calcitrans* (Linnaeus) and *Phormia regina* (Meigen) all take sugar and protein-containing meals, the former to suport life, the latter for ovarian development [Knuth (124); Séguy (129); Derbeneva-Ukhova (130); Kuzina (131); Rasso & Fraenkel (132)]. As before, however, there are exceptions; for example, *Siphona* and many Hippoboscidae feed on blood alone. The important difference, however, is that both sexes of these flies, whether vertebrate- or insect-eating, carrion-feeding or vegetarian, take the protein-containing meal; and they obtain this meal in many ways other than by biting. Again, throughout these large groups, the mandibles are lacking, both in biting species and in others. The laciniae persist in some families; but the cephalic pumps, differing between the Heterodactyla and Cyclorrhapha, differ also from those of both lower groups. The biting forms pierce in a variety of ways [Snodgrass (3)]; and both for this reason and because of its irregular distribution in the system, bloodsucking is evidently, in most instances at least, a secondary development.

The experimental results indicate that the normal span of life, of both sexes, can be attained on a carbohydrate diet alone, as is the case in the lower flies. If this is correct, the protein-containing meal in all the Diptera is related basically to reproduction, and other vital functions requiring protein are supported primarily from larval reserves. It could perhaps be shown that this characteristic differentiates the Diptera from other orders, e.g., the Mecoptera and Coleoptera.

In respect to feeding habits and the possession of mandibles, the Diptera may therefore be divided into two groups that cut across the customary divisions: the Nematocera and the Brachycera Homoeodactyla falling in one, the Brachycera Heterodactyla and Cyclorrhapha in the other. This is not to deny the distinction between the Nematocera and the Homoeodactyla, which is evident in details of the mouth parts, the sucking pumps and other features; rather it suggests that they are on a comparably primitive level, which was maintained in the nematoceran stock but in the brachyceran un-

derwent transformation at a certain level. This transformation gave rise to the remaining Diptera: nonmandibulate, protein-feeding in both sexes and using a great variety of protein sources other than live animals.

Primitive Diptera: Diptera and Mecoptera.—It has been implied throughout that the nonbiting forms of the lower Diptera are secondary. This is contrary to a common opinion; for example, Mayer (65) and Mackerras (113) envisage the blood-sucking habits of the Ceratopogonidae, Tabanidae, and Rhagionidae to have originated within each family, perhaps on more than one occasion. However, in families such as Culicidae and Tabanidae the nonbiting forms occur as species, genera or tribes within otherwise biting groups; in the Psychodidae and Rhagionidae, a smaller number of biting forms are scattered in two or more major sections. These facts alone suggest that the biting forms are more primitive; and since the biting mouth parts are complex and uniform they certainly have a common origin. Similarly, many of the biting families are grouped into higher units such as the Culiciformia and Tabanoidea [Hendel (133); Hennig (98)] and, particularly when the related families with reduced mandibles are considered, it seems likely that in these larger groups also biting is primitive. The Chironomidae, for instance, should thus be regarded as a family of Culiciformia with reduced mouth parts. Further, there are an identity of habit and important resemblances in the mouth parts of the families ranged in the Nematocera and those in the Homoeodactyla. This suggests that the original Diptera were biting flies. Such an opinion was briefly indicated by Edwards (134). It is supported by Snodgrass' demonstration (3) that the biting mouth parts are homologous with those of typical insects; and by Tillyard (135) and Imms (1), who showed that among the Mecoptera, a more primitive group closely related to the Diptera, one family, the Nannochoristidae, resembles the biting flies in two additional and rather striking details. In this family only a single maxillary lobe persists, as in all Diptera, and a peculiar sense organ occurs on the third palpal segment, as also in the Blepharoceridae, Ceratopogonidae and Simuliidae. It may be concluded that these flies are, in respect of their mouth parts, directly connected with the Mecoptera.

It does not follow that the lower biting flies are primitive in other respects, but support for this suggestion also is available. It is commonly held, on venational and other grounds, that the Tanyderidae—a small family of nonbiting, tipulid-like flies—are a very archaic group, and some authors hold the same opinion of the Psychodidae [Tillyard (136); Hendel (133), Edwards (134), Hennig (98)]. Except Tillyard (136), most authors have associated the Psychodidae and the Tanyderidae and placed them close to the culicimorphs; that is, the biting Nematocera are considered closely allied to the forms that on traditional grounds have been identified as the most primitive of present-day Diptera. Further, the Psychodidae are themselves, in all probability, a biting group; and Crampton (137) discovered

that the pupa of the Tanyderidae possesses mandibles. It is therefore no great step to suggest that the biting Nematocera, as a group, are the closest existing representatives of the original Diptera.

Whether the early Diptera were originally predators of vertebrates or of insects is difficult to decide. When they originated, in the Permian [Tillyard (135)], terrestrial forms of both groups were available.

The Mecoptera themselves show a duality of feeding habits; the insectivorous Bittacidae and the scavenging Panorpidae both feed also at flowers [Currie (138); Carpenter (139)]. The distinctions, however, between the Mecoptera and Diptera should not be minimized. In the former the labrum and hypopharynx are not apposed to form a sucking tube; there is no crop, the organ that serves for the storage of sugar solutions in Diptera [Waterhouse (126)]; and they possess a proventriculus with cuticular hairs, lacking in the Diptera. Most important, perhaps, the protein-containing meal is taken by both sexes; in the origin of the Diptera this was restricted to the female sex, although the specialized members of one stem later regained, or at least simulated, a mecopteran economy. It may be noted, in conclusion, that, in all these points in which the Mecoptera and the Diptera differ, the Mecoptera and the Siphonaptera, another order commonly included in the panorpoid complex, are alike. (For further discussion of the panorpoid complex see review by Hinton in this volume.)

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RESISTANCE OF PLANTS TO INSECTS[1,2]

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Increased interest in resistance of plants to insects has been evident recently following the lull in agricultural research of the war years and the more recent intense interest in the new organic insecticides. The widespread development of resistance to many of these insecticides by pest species has caused thoughtful entomologists to realize that *all* possible means must be employed in insect control. An important part of any well-rounded insect control project should be the search for sources of insect resistance, and the use of varieties having such resistance in reducing the populations of insects and the damage done by them. Therefore, these aspects of the plant-insect relationship will be emphasized.

Plants that are inherently less damaged or less infested than others under comparable environmental conditions in the field have been called *resistant.* The first analysis of why plants are resistant indicates that three basic components are concerned. In the first place plants may be *nonpreferred* for oviposition, shelter or food, primarily because of the lack of certain qualities which, for example, may be minute in quantity if the property is chemical in nature. Secondly, resistant plants may affect the biology of the insect adversely, a component of resistance called *antibiosis.* Thirdly, resistant plants may be *tolerant,* surviving under levels of infestation that would kill or severely injure susceptible plants. These three components, as will be discussed later, are in themselves complex. They are concerned with effects rather than causes although sometimes similar results do come from diverse causes.

This review covers publications on the phases of resistance that have come to the writer's attention between publication in 1951, of a book [Painter (137)] and May, 1957. Many additional reports on resistance, mostly short, are not included in the bibliography. Some general aspects of subjects related to insect resistance, such as physiology of feeding [Barnes (18); Chatters and Schlehuber (47); Hocking (87); Lipke & Fraenkel (113); Smith *et al.* (171), etc.], and the chapter on the nutrition of phytophagous insects by Friend in this volume, together with the papers which they review, are highly pertinent to an understanding of resistance and should be consulted. The same may be said of studies on insect behavior in relation to hosts [Brues (35); Dethier (61 to 64); Kennedy (99); Thorsteinson (181, 182, 183)]. A few general papers dealing with insect resistance have been published

[1] The survey of the literature pertaining to this review was completed in May, 1957.

[2] Contribution No. 688, Department of Entomology, Kansas Agricultural Experiment Station, Manhattan.

TABLE I

Insects and Crops Being Studied for Resistance in the United States, 1955

Crop	Insect being studied		States where problem is being studied*	Lit. Ref., where available†
	Common Name	Scientific Name		
Alfalfa	Spotted alfalfa aphid	*Therioaphis (Pterocallidium) maculata* (Buckton)	Ariz., Ark., Calif., Colo., Ind., Iowa, Kans., Nebr., Nev., N. Mex., Okla., S. Car., S. Dak., Utah, Va., Wisc., USDA	(30, 69, 83, 148, 174, 175, 192)
	Pea aphid	*Macrosiphum pisi* (Harris)	Calif., Kans., Nev., USDA	
	Potato leafhopper	*Empoasca fabae* (Harris)	Ark., Ind., Minn., Nebr.	(60, 180)
	Three-cornered alfalfa hopper	*Spissistilus festinus* (Say)	Ark., S. Car.	
	Clover leafhopper	*Aceratagallia sanguinolenta* (Provancher)	S. Car.	
	Meadow spittlebug	*Philaenus leucophthalmus* (L.)	Ind.	(195)
Barley	Greenbug	*Toxoptera graminum* (Rondani)	Kans., Okla., Tex., USDA	(57, 59)
	Hessian fly	*Phytophaga destructor* (Say)	Calif., Ind., USDA	(86)
	Apple grain aphid	*Rhopalosiphum fitchii* (Sanderson)	Calif.	
Beans	Mexican bean beetle	*Epilachna varivestis* Mulsant	N. Car.	
Cantaloupes	Striped cucumber beetle	*Acalymma vittata* (F.)	N. Car.	
	Spotted cucumber beetle	*Diabrotica undecimpunctata howardi* Barber	N. Car	
Collards	Harlequin bug	*Murgantia histrionica* (Hahn)	N. Car.	
Corn, field, sweet and pop	Corn ear worm	*Heliothis zea* (Boddie)	Ala., Fla., Ga., Ind., Kans., Md., Miss., N. Car., Okla., Tex., USDA	(70, 71, 173, 190, 191, 193, 197)
	European corn borer	*Pyrausta nubilalis* (Hübner)	Ala., Fla., Ill., Iowa, Mich., Minn., Ohio, Penn., Wisc., USDA	(6, 7, 65, 67, 88, 131)
	Rice weevil	*Sitophilus oryza* (L.)	Ala., Fla., Ga., N. Car., USDA	(73, 74)
	Corn leaf aphid	*Rhopalosiphum maidis* (Fitch)	Kans., Penn.	(188)
	Southwestern corn borer	*Zeadiatraea grandiosella* (Dyar)	Kans., Okla., USDA	
	Sugarcane borer	*Diatraea saccharalis* (F.)	Okla., USDA	
	Corn silk fly	*Euxesta stigmatias* Loew	Fla.	
	Grasshoppers	*Melanoplus* spp.	Kans.	
	Japanese beetle	*Popillia japonica* Newman	Penn.	(55)
Cotton	Boll weevil	*Anthonomus grandis* Boheman	Ark., La., N. Car.	
	Thrips	various species	Ark., Ga.	(17)
	Cotton aphid	*Aphis gossypii* Glover	Ark.	
	Pink boll worm	*Pectinophora gossypiella* (Saunders)	La., Tex.	(34)
Oats	Greenbug	*Toxoptera graminum* (Rondani)	Okla., Tex., USDA	(57, 59)

* Members of U. S. Department of Agriculture are cooperating either through the plant breeder or entomologist, or by furnishing plant material in certain projects other than those reported in the table.

† See also more detailed reports in the text and references in Table II and Painter (137). Thanks are due to the many who replied to the questionnaire for much of the information recorded here and in Table II.

TABLE I (*Continued*)

Crop	Insect being studied		States where problem is being studied*	Lit. Ref., where available†
	Common Name	Scientific Name		
Onion	Onion maggot	*Hylemya antiqua* (Meigen)	Wash.	
	Onion thrips	*Thrips tabaci* Lindeman	Ohio	
Peanuts	Thrips	various species	Fla.	
Pecan	Black pecan aphid	*Melanocallis caryaefoliae* (Davis)	N. Mex.	
Pepper	Pepper maggot	*Zonosemata electa* (Say)	N. Car.	
Potato	Potato leafhopper	*Empoasca fabae* (Harris)	Ohio, Minn.	(114, 149, 169, 176)
	Green peach aphid	*Myzus persicae* (Sulzer)	Me.	
Rhodes-grass	Rhodes-grass scale	*Antonina graminis* (Maskell)	Tex.	
Sorghum	Chinch bug	*Blissus leucopterus* (Say)	Kans., Neb., Okla.	(58)
	Sorghum midge	*Contarinia sorghicola* (Coquillett)	Ga.	
	European corn borer	*Pyrausta nubialis* (Hübner)	Ala.	
	Corn leaf aphid	*Rhopalosiphum maidis* (Fitch)	Kans.	(45, 94)
Squash	Striped cucumber beetle	*Acalymma vittata* (F.)	Kans.	
	Squash bug	*Anasa tristis* (DeGeer)	Kans.	
	Spotted cucumber beetle	*Diabrotica undecimpunctata howardii* Barber	Kans.	
Sugar cane	Sugarcane borer	*Diatraea saccharalis* (F.)	La.	(125, 189)
Sweetclover	Sweetclover weevil	*Sitona cylindricollis* Fåhraeus	Ind., Minn., Nebr.	(196)
	Sweetclover aphid	*Myzocallidium riehmi* Börner	Kans., Minn.	(147, 148)
Tobacco	Green peach aphid	*Myzus persicae* (Sulzer)	Ky.	
Wheat	Hessian fly	*Phytophaga destructor* (Say)	Calif., Ga. Ill., Ind., Kans., Ky., Mich., Mo., Nebr., N. Y., Penn., Wisc., USDA	(2, 41, 137) (143, 177)
	Greenbug	*Toxoptera graminum* (Rondani)	Kans., Okla., Tex., USDA	(57, 144)
	Wheat stem sawfly	*Cephus cinctus* Norton	Mont., N. Dak., USDA	(72, 135)
	Wheat jointworm	*Harmolita tritici* (Fitch)	Ind., Mo., USDA	(97)
	European wheat stem sawfly	*Cephus pygmaeus* (L.)	Pa.	
	Wheat strawworm	*Harmolita grandis* (Riley)	Kans.	

[Chesnokov (49, 50, 51); Hayes, *et al.* (84); Horber (90); Müller (130); Packard & Martin (136); Painter (138, 139, 140); Pinotti (150); Rawat (155)]. Some of them include extensive bibliographies.

Research on Resistance Now in Progress

The study of insect resistance characteristically is a long-time project. The production of a new variety which involves hybridization followed by selection, usually requires a minimum of six to ten years, although this time may be shortened when more than one crop can be grown each year. Detailed reports of such resistance projects are usually given only near the end of the breeding and testing program. There are, however, frequently brief notes in annual reports, newsletters, confidential mimeographed reports, etc. To supplement published sources of information, 222 questionnaires were

sent to entomologists and plants breeders at all state agricultural experiment stations and to U. S. Department of Agriculture laboratories known to be working on insect resistance in the United States. No questionnaires were sent to other countries. Ninety-four forms were returned with often two or more persons collaborating in the replies. Thirty-six states, including the federal laboratories, are represented.

A summary of part of the information gathered, together with references to published reports, where available, is given in Table I. Fifty-two insect-crop relationships were reported for 20 crops. This does not indicate the full extent of work on insect resistance in the United States. In addition, observations on most natural insect infestations in variety plots were mentioned as being taken when possible by agronomists. Probably some persons making resistance studies failed to reply or were not contacted. Knipling (102) reported that about 4 per cent of the research funds for the Entomology Research Division, Agricultural Research Service, United States Department of Agriculture for 1956–57 was being spent on the study of insect resistance in plants. This is the smallest amount except one, to be spent on the seven divisions of applied entomology mentioned.

One interesting feature of the replies to the questionnaires was the high interest (in 16 states) indicated in study of resistance to the spotted alfalfa aphid which has been present in the United States only three years (Table I). This interest probably arises from the insect's destructiveness, transitory nature of available chemical control, rapid spread into 30 states by the end of 1956, and the early and widespread evidences of sources of resistance in the variety Lahontan (see literature references, Table I and II). In addition to Lahontan, individual plants in some susceptible varieties proved to be resistant [Harvey & Hackerott (83)]. Selection and increase of these plants may quite possibly speed up the availability of regionally adapted varieties. Another synthetic variety, New Mexico 16, is a promising resistant variety that is being increased [Dobson & Watts (69)].

Lahontan alfalfa is also resistant to the stem nematode and to bacterial wilt but its range of agronomic adaptation is only partially known. Only part of the Lahontan seedlings are resistant to spotted alfalfa aphid [Harvey & Hackerott (83)], so resistance to nematodes is probably not governed by the same genetic factors as resistance to the aphid.

Twelve experiment stations reported progress on resistance to hessian fly. This interest is probably partly the result of the successful use of wheats resistant to hessian fly in Kansas and California. In these two states and in Indiana the entomological research has been in cooperation with the United States Department of Agriculture. Beside the original search for the sources of resistance, many thousands of plants and hybrid selections are exposed annually to fly infestation to detect resistant strains. Agronomic tests of the selected hybrids have been done at three stations as well as in cooperating states throughout the territory infested by the hessian fly. It has been relatively simple to transfer resistance to desirable agronomic types but the need

to include, in addition, the complex milling and baking characteristics and disease resistance, makes the breeding of wheats resistant to hessian fly a more difficult problem than the perfection of insect-resistant varieties in many other crop plants.

Ten stations reported work in progress in breeding field, sweet, and pop corn in attempts to incorporate resistance to corn earworm. This insect does widespread damage yearly, especially in the southern and western parts of the corn-growing area. So far, chemical control has proved quite expensive and not particularly effective against heavy populations. For those reasons particularly, the study of resistance has been important. In sweet corn, where a product relatively free from damage is required, a combination of resistant varieties with chemical control has been effective [Wene *et al.* (193)].

Nine experiment stations reported studies in progress on resistance to European corn borer. Early work on this problem was done in Ohio both at the United States Department of Agriculture Laboratory at Toledo and the State Experiment Station at Wooster. As the borer invaded new territory to the west, the federal studies were moved to Ankeny, Iowa, where more than 5000 strains of corn are artificially infested each year [Dicke (65); Dicke & Penny (67)]. This artificial infestation involves rearing moths and producing hundreds of thousands of egg masses for hand infestation for use both in Iowa and in other state experiment stations. Similar artificial infestation is being done in Minnesota where 250,000 egg masses were produced in 1950 [Holdaway (88)]. Studies by federal entomologists have been in cooperation with the corn breeders in most of the states where borer infestations are present. In addition, much detailed study has been made by state experiment stations of Ohio, Minnesota, and Pennsylvania. The laboratory work at Wisconsin has been directed toward analyzing the possible causes of resistance to the borer. Several commercial hybrid corn companies raise corn borer moths, to produce egg masses for artificially infesting a large number of plants to test inbreds and hybrids they are studying. Corn breeders in these companies also record damage by other insects to strains of corn they are testing.

The studies of resistance to other insects recorded in the United States has been of more limited scope (Table I). Almost all studies, however, involve active cooperation between entomologists and the plant breeders.

Important work in resistance is being done outside the United States but recent information regarding it has been difficult to obtain by way of either published reports or questionnaires. According to published reports seen, areas where considerable work is being done and subjects studied include among others: Argentina, resistance to greenbugs in small grains [Arriaga (13, 14)] and resistance to grasshoppers [Rosbaco (161)]; Australia, resistance to cotton leafhopper and other insects in cotton [May (126)]; Canada, resistance to wheat stem sawfly [Roberts (158)], resistance in peas to pea aphid [Maltais (122)]; England, resistance to woolly apple aphid, *Eriosoma lanigerum* Hausman (Massee (123, 124)]; East Germany, resistance to aphids in

TABLE II

Some Known Insect-Resistant Crop Varieties Being Grown on Farms in the United States*

Crop	Variety Name	Insect resisted	Year first recommended or distributed	Area of use or recommendation and estimated acreage in area concerned	Literature reference where available
Alfalfa	Vernal	Leafhopper	1953	34% of Wisconsin acreage	
Alfalfa	Ladak	Pea aphid	1937	Kansas; acreage small	
Alfalfa	Lahontan	Spotted alfalfa aphid	1954–56	Trace to 10% in Calif., Nev., Utah, Ark.	(174, 175)
Barley	Dicktoo	Greenbug	1952	Kansas	(141)
Barley	Kearney	Greenbug	1954	Texas Panhandle	(10)
Beans	Wade	Mexican bean beetle		About 50% in N. Car. of bush snap beans	
Corn	Ks. 2234	Grasshoppers	1943	Small acreage in Kansas	
Corn	Ks. 1859	Corn leaf aphid	1950	Increasing in Kansas	(140)
Corn	Calumet	Earworm		70% in lower Rio Grande valley	(193)
Corn	Paymaster	Earworm		20% in lower Rio Grande valley	
Corn	Dixie 11	Earworm	1946	50% in southern part of South eastern states	(70, 81)
Corn	Dixie 18	Earworm	1948		
Corn	Dixie 18	Rice weevil	1948–50	Ala., N. Car., Fla., Miss., Ga.	(8, 73, 74)
Corn	Coker 811	Rice weevil	1948–52	N. Car., Ala., Fla.	(8)
Corn	Victory Golden	Sap beetles		15% in Maryland	(54)
Corn	Hoosier Gold	Sap beetles		1% in Maryland	(54)
Corn	L316, Oh45, etc.	European corn borer		98% resistant hybrids in Ohio, less in other states (see text)	(66, 67, see text)
Cotton	Empire	Thrips	1944	35% of Ga. acreage	(17)
Sorghum	Atlas	Chinch bugs	1928	Kans. Nebr. Okla. leading sorgo in acreage	(137)
Sorghum	Axtel	Chinch bugs		Nebraska	
Sorghum	Redbine 60	Chinch bugs		Nebraska	
Sorghum	Dwarf Kafir 44-14	Chinch bugs	1950	Kansas, Okla.	(46)
Sorghum	Piper sudan	Corn leaf aphid	1950	80% of Wisc. acreage	(94)
Squash	Butternut	Squash vine borer		New Jersey	
Sugar Cane	F. 31-962	Sugarcane borer	1936	20% in Fla. 4% elsewhere	
Sugar Cane	C.P. 34-79	Sugarcane borer	1942	50% in Fla. 1% elsewhere	(125)
Sugar Cane	C.P. 34-120	Sugarcane borer	1942	1% in U. S.	
Sugar Cane	C.I. 38-32	Sugarcane borer	1944	2% in Fla., trace elsewhere	
Wheat	Mida	Grasshopper		50,000 acres in Wyo.	
Wheat	Pawnee	Hessian fly	1942–45	Nebr., Kans., Okla., leading variety in acreage since 1949 in U. S.	(137)
Wheat	Big Club 43	Hessian fly	1944	98% of acreage in fly infested area of Calif.	(178)
Wheat	Ponca	Hessian fly	1951	13% in Kansas, 5% in Okla., 4% in Ill., 5% in Mo.	(112)
Wheat	Dual	Hessian fly	1956	60,000 acres in Ind., 1¼% in Ill., some in Ohio, Penn.	(11, 41)
Wheat	Russell	Hessian fly	1956	20% in Wisc.	(12)
Wheat	Todd	Hessian fly	1956	Ky.	
Wheat	Rescue	Stem sawfly	1948	15% in Mont, 1 to 2% in N. Dak.	(43)
Wheat	Chinook	Stem sawfly	1952	1% in Mont., trace in N. Dak.	(9)
Wheat	Rego	Stem sawfly	1957	Mont.	(12a)

* Information on some of the older varieties may be found in Painter (137); see also more detailed reports in the text and references in Table I. Acreage estimates were those given in replies to questionnaire.

beans [Müller (129, 130)]; France, Germany, Holland, resistance to Colorado potato beetle, *Leptinotarsa decemlineata* (Say) [Boczkowska (32, 33); Buhr (36); Chauvin (48); Schaper (165); Torka (184, 185)]; India, resistance to an anthomyiid, *Atherigona indica* Malloch, in sorghum [Pennaiya (153, 154)]; Japan, resistance to rice insects [Kawada (98); Nishijima (132, 133, 134); Yuasa (198)] and resistance to soybean insects [Ishii (96)]; Mexico, resistance in beans to insects [McKelvey (119); McKelvey *et al.* (120)]; New Zealand, resistance to garden and truck crop insects [Lamb (108, 109)]; Pakistan, resistance to cotton leafhoppers [Afzal & Ghani (1)]; Sudan, resistance to leafhoppers and other insects in cotton [Knight (101)]; Switzerland, resistance to chloropids in small grains [Horber (91, 92)].

Insect Resistant Varieties Being Grown in the United States

Judging by its scant mention in recently published entomological text books, the extent to which insect-resistant plant varieties are grown in the United States is not generally realized by entomologists. Many resistant varieties (Table II) have originated from long-planned research. Sometimes low levels of resistance were discovered in older varieties and appreciated when new and more susceptible varieties were introduced. Some, such as Lahontan alfalfa, have been found to be resistant to an insect after being distributed or recommended because of other desirable characters. Table II presents information regarding some of the 30 to 50 varieties of crop plants carrying known insect-resistant factors and being grown at the present in the United States. These varieties range from some that have just been introduced and are being grown on small acreages, to such varieties as Atlas Sorgo the leading forage sorghum in the Midwest. Atlas Sorgo was introduced in 1928 and still carries resistance to chinch bugs.

Virtually all the varieties recorded represent important improvements in other respects in addition to the insect resistance. An experiment station cannot ordinarily afford to recommend or distribute varieties that are not superior. There are two kinds of exceptions to this. First, when a variety is grown outside its area of adaptation or recommendation, it may not be considered superior in all respects. For example, when the hessian fly resistant hard wheat, Ponca, is grown in soft wheat growing territory outside the area of recommendation, it retains its fly resistance and agronomic value, but is greatly disliked by millers in that area since it does not fit their regular milling program. A second exception is exemplified by Rescue wheat which is grown on several million acres in North America because it has been, with Chinook, the best available wheat carrying resistance to wheat stem sawfly, for which no other practical control is known. In the absence of the insect, Rescue often does not compete in yield with susceptible varieties. It is less desirable in milling quality than many susceptible varieties it replaces but its use permits the profitable growing of wheat in infested areas until more desirable sawfly resistant varieties become available.

Corn is unique in comparison with many other crops in the use of first generation hybrids for farm grain production. This use has given rise to an

extensive industry in the production of hybrid corn seed supported by independent research programs. Both hybrids and constituent inbreds must be tested for insect resistance. Usually at least two or three of the four inbreds must be resistant to give a resistant hybrid. Hybrid seed corn companies at first used insect-resistant inbreds and combinations developed by experiment stations. Later, in their own corn-breeding programs, they developed and used, in addition, their own inbreds and hybrids often recording all under secret pedigrees. Hence, it is often impossible to tell to what extent known insect-resistant inbreds have been used in hybrids in the corn growing areas.

The development of earworm-resistant corn has been especially valuable in the South. Such strains have contributed to the profitable growing of sweet corn in many areas [Walter (190, 191); Yarnell (197)]. The selection of certain inbreds which carry genetic factors for silks that are lethal to young earworm larvae has been an important find [Walter (191)]. The combination of Calumet sweet corn with the use of insecticides has given satisfactory control in the Rio Grande Valley where satisfactory control could not be achieved by use of either resistant variety or insecticide alone [Wene *et al.* (193)]. In field corn in the South it is important to have resistance both to the rice weevil and the corn earworm. Such resistance is present to a greater or less degree in several hybrids. Coker 811, which is listed in Table II as resistant to the rice weevil, is reported also to carry earworm resistance. According to Douglas & Eckhardt (70),

> Dixie 18 is a yellow hybird that yields well, is resistant to both the earworm and the rice weevil, and has excellent quality of grain. It is the leading yellow hybrid of the South . . . Dixie 11 is a white hybrid, having intermediate resistance to both the earworm and the rice weevil. It yields well and produces good-quality corn.

They also list La. 521 as a white hybrid having medium resistance to earworm and rice weevil. Information is given by them on five highly resistant white inbreds, L501, L503, F1, F2 and Mp313, and a highly resistant yellow inbred, F6.

A number of hybrids and inbreds carrying varying degrees of resistance to the European corn borer have been developed for use under the varied conditions of the central United States. Consequently, hybrids in use are discussed below instead of being in the table. The following inbred lines contribute resistance to hybrids principally in the whorl stage: L317, B2, Oh7, Oh40B, Oh41, Oh43, Oh45, Oh51A, W10, W22, W23, A392, R4, R61, Hy, WR3; and the following contribute tolerance in the form of low percentage of stalk breakage: B14, B15, B30 [Dicke & Penny (66)]. Attempts are under way to combine these two characteristics in the same usable inbreds. Some of the earliest work on resistance to the European corn borer was done in Ohio, where the borer resistant hybrids K64, W64, C54 were distributed in 1949, and C51 in 1952. It was estimated that these hybrids are grown on at least 500,000 acres. The inbreds, Oh43 and Oh45, which occur in these hy-

brids are believed to be used extensively in commercially produced, closed pedigree borer resistant hybrids. Pennsylvania requires many kinds of corn because of the varied ecological conditions. The following hybrids recommended for various areas are reported to carry excellent resistance to European corn borer and corn leaf aphid; Pa 444, Pa 602, Pa 602A, Pa 612, Pa 711, Oh W64, and Pa 850. In Illinois, inbreds carrying resistance to the European corn borer and recently released to seedsmen include R71, R109B, R113, R168. In Minnesota, hybrids Min. 411 and Min. 412 were recommended in 1953 and Min. 414, Min 511, and Min. 509 in 1955. These hybrids are superior to previously recommended ones in other characters as well as borer resistance. The hybrid C92 has been released and is grown in central and southern Iowa. It would class as having intermediate resistance to first brood European corn borer larvae.

The resistance of sorghums to chinch bug has been studied especially in Oklahoma [Dahms & Sieglinger (58)] supported by observations in the sorghum breeding nurseries in Kansas and Nebraska. An important feature of the recent work has been the development among grain sorghums, which can be harvested by a combine, of varieties that are less susceptible to chinch bugs than the first combine sorghums produced [Painter (137)]. Redbine 60 and Dwarf Kafir 44–14 (Table II) are examples of such combine sorghums. They are much more resistant than Wheatland or Dwarf Yellow Milo but still below the level of resistance represented by Atlas.

As indicated in Table II, Pawnee wheat, which carries some resistance to hessian fly, became the leading wheat in acreage in the United States in 1949. The early history of this variety is given by Painter (137). The variety reached this high acreage primarily because of its general agronomic superiority and has continued to occupy this position, although it is now decreasing in acreage according to a recent report [Salmon & Reitz (164)]. Pawnee wheat does not give a much lower level of infestation than the varieties it displaced east of Kansas but often preserves its tolerance to the hessian fly. It has continued to show a satisfactory level of resistance in central Kansas and Nebraska. Ponca wheat, which is suited to southeastern Kansas, where Pawnee is less resistant to hessian fly, has also spread into the nearby eastern states and retains its resistance to hessian fly in that area. The early history of Ponca was given by Painter (137), p. 162–163, under the designation Kawvale – Marquillo × Kawvale – Tenmarq, C.I. 12128. Farm use of Ponca has spread more slowly, primarily because its superiority—except in hessian fly and leaf rust resistance—over Pawnee has been less than the superiority of Pawnee over the varieties it replaced. Production of the soft winter wheat variety, Dual, climaxes some 32 years of breeding and research at the Indiana station in cooperation with United States Department of Agriculture entomologists [Caldwell *et al.* (41)]. The name of the variety refers to its use for pasture and forage as well as for grain. In both respects it is a high producer. Dual carries resistance to leaf rust and soil borne mosaic as well as to hessian fly and thus provides many advantages for use in Indiana as well as in

neighboring states. The winter wheat variety, Todd, and the spring wheat variety, Russell, carry resistance from the same source (gene H_3) as Dual and originally were developed in part from the same research program with later development and testing in Kentucky and Wisconsin.

Varieties of wheat resistant to wheat stem sawfly have been developed by Canadian workers [Rescue and Chinook (Table II)]. In the northern United States they are often out of their region of best adaptation, but give considerable protection against the insect. Extensive research is under way both in the United States and Canada toward the production of improved sawfly resistant wheats.

Resistant Varieties as Insect Control Measures

The effect of insect resistant varieties in reducing damage is a conspicuous result which can often be readily pictured [Painter (137)]. Douglas & Eckhardt (70) stated that the percentage of kernels damaged by corn earworm in Dixie 18 was only about one-sixth that of a commonly used open-pollinated variety [see also Douglas *et al.* (71)]. Daniels *et al.* (59) picture the differences in injury by greenbugs to resistant and susceptible varieties of barley. Similar differences are frequently observed in the cases of comparisons between resistant and susceptible varieties growing side by side. The effect of growing an insect resistant variety on the population of the insect resisted is less easy to measure and to document, but evidences of that effect have been frequently observed. When insects are reared on resistant varieties in the laboratory the reduction in fecundity, early death of adults, and general inability to maintain a population are matters of fairly common observation. They are most readily evident when aphids are confined on a resistant plant. In a study of the spotted alfalfa aphid, Harvey & Hackerott (83) found that when placed on each leaf of nine resistant plants, 20 aphids decreased after five days to an average of less than two aphids per leaf, while on the susceptible plants the same number of aphids increased to an average of 60 per leaf. In a study of the corn leaf aphid, Cartier & Painter (45) found that the biotype KS 1 gave almost no reproduction when caged on resistant sudan while biotype KS 2 reproduced on resistant sudan much more slowly than on susceptible sorghums. Studies in the field in Kansas at several intervals beginning with 1921 [Painter (137)], have indicated that sudan in general has been relatively free from large colonies of corn leaf aphids. Thus the effects seen in the laboratory often may be found duplicated in the field. Maltais (122), working with the pea aphid, found three times as many aphids in the field on susceptible varieties as on resistant ones in each year during a nine-year study.

Hessian fly.—One of the best recorded cases of the effect of a resistant variety on an insect concerns the hessian fly. The hessian fly resistant variety, Big Club 43, which was released to California farmers in 1944, together with the resistant variety Poso 42, released earlier, replaced susceptible wheat varieties in the hessian fly infested areas, reducing the fly popula-

tion to such an extent that by 1946 further studies of the fly and breeding for resistance had to be abandoned because of lack of insect material. This was in an area where for each year from 1920 to 1944, infestation levels of 50 to 100 per cent of the plants infested had been recorded. C. A. Suneson, research agronomist at Davis, California, reported on the questionnaire that in the last survey in 1954, in 16 fields of Big Club 43 no fly puparia were found, while in a single field of a susceptible variety a single puparia was located. Thus, this resistant variety was effective and has remained protective despite a small residue of susceptible varieties in the area. A similar situation has developed in central Kansas in the area where Pawnee has been widely grown. As previously reported [Painter (137)], as the total acres of Pawnee sowed increased, the population of fly decreased in spite of extremely favorable weather conditions for the insect during the five years preceding 1948. Since 1948 the weather has been unfavorable to the development of this insect [Painter (139)]. Under the combination of unfavorable weather and resistant variety the hessian fly population has decreased to the point where it has been almost impossible to find any evidence of the insect even in the most favorable locations. This reduction has occurred in an area where for many years the insect annually caused heavy losses in wheat, even during the drought years of the 1930's. Since 1949 in Kansas it has been possible to carry on the study of hessian-fly resistance only in the greenhouse with fly populations maintained under artificial conditions. The reduction in hessian-fly populations occurred even though, during most of the years, susceptible wheats occupied ten to fifty per cent of the wheat acreage in various counties. At the present time the fly resistant Pawnee and Ponca, together, make up about half the wheat acreage in the eastern half of Kansas. With the return of weather more favorable to the fly this level of resistant acreage may not be sufficient to keep down the fly population.

European corn borer.—The effect of resistant hybrids in reducing the number of surviving borers on a plant in experimental plots has been reported frequently. This reduction occurs primarily during the feeding of first instar larvae in the whorl of the plant. Dicke & Penny (66) reported that resistant hybrids commonly have 50 to 60 per cent less borer survival than susceptible ones. Where resistant varieties are widely planted such a reduction in survival should be noticeable as causing a general reduction in the population of the insect. Neiswander (131) listed the widespread use of resistant hybrids as one of the reasons the population of the European corn borer had been only about half as high in Ohio as in Iowa. In Iowa there had been insufficient time after the arrival of the insect to develop borer-resistant adapted hybrids. At the present time a large proportion of hybrids grown in Ohio carry more or less resistance to the European corn borer. G. H. Stringfield, corn breeder in Ohio, in answer to a question regarding the effect of the resistant varieties on the insect resisted, stated, "The corn borer hazard has been reduced to a minor problem on those farms that use these (resistant) hybrids." T. H. Parks, formerly extension entomologist

in Ohio, in response to the same question, stated that the growing of certain adapted resistant varieties "makes the use of insecticides unnecessary" against the European corn borer in field corn. The increasing use of resistant varieties in other states holds promise of the further reduction in the damage done annually by this insect.

In contrast to this developing situation in the United States, corn hybrids from this country tested in Europe were reported to be more susceptible to the European corn borer than the varieties then being grown there [Angulo-Busquets (3, 4); Baldoni (16); Gandori & Rota (80)]. The hybrids concerned quite probably were those classed as susceptible in the United States since that was the classification of those readily available until recently. There is a possibility that different biotypes of the borer were involved since corn borer populations showing host preference differences are known.

In assessing the effect of a resistant variety on an insect population, it is important to remember that the effect is likely to be cumulative. Even with a variety which reduces the population by only 50 per cent each generation, it will not be many generations before the insect is in a precarious situation from the standpoint of survival. At such a point, other natural forces may further reduce its numbers.

The Basis and Modifiability of Resistance

Problems regarding the cause or basis of insect-host relationships are always foremost early in any study of resistance. Often a first question is whether plants surviving a severe infestation are really resistant. Usually this can be best determined by testing progeny of such plants in contrast with known susceptible ones. The next step in the study of the basis of resistance involves a determination of the proportions in which the three components, nonpreference, antibiosis, and tolerance, are present to give the differential injury seen in the field.

Basic to these and further studies on resistance is a thorough understanding of the biology and behavior of the insect in relation to its host plant. A few examples may be given of the type of research needed. Refai *et al.* (156, 157) have contributed materially to knowledge of the basis of hessian fly resistance in wheat through a study of feeding of the insect and biochemistry of the hosts. Their studies suggest the importance of hemicellulose and hemicellulase in hessian fly resistance. Diehl & Chatters (68) studied the feeding damage done by the spotted alfalfa aphid. Kennedy & Booth (100) recorded the feeding preferences of the bean aphid, *Aphis fabae* Scopoli, on different parts of the same plant. Roberts (158) and Holmes (89) analyzed the method of feeding and components involved in wheat stem sawfly resistance. Ishii (96) gave a detailed analysis of the relation of the cowpea weevil, *Callosobruchus chinensis* (Linneaus), to various kinds of beans. Hensley & Arbuthnot (85) made a study of the feeding and migration of the southwestern corn borer larvae, *Zeadiatraea grandiosella* (Dyar).

A number of basic studies have been made on the European corn borer

and corn. Burditt (39) examined the similarity between laboratory and field studies of resistance. Bell (29) showed that there are certain cells of the corn plant on which the corn borer begins feeding. The number of these cells differed in the resistant and susceptible corns studied. Cox (56) in a study of the localized area in the corn plant where resistance may occur, showed striking differences in various inbreds, in the feeding of both first and second broods. Luckmann (118) studied in detail the relation of the age of the plant as measured by tassel development, to borer survival. Chiang *et al.* (52) gave an analysis of the second generation feeding of the European corn borer; while Patch *et al.* (145) analyzed the damage done by the second generation to various hybrids and inbreds. Many of the factors studied by these workers on the biology of the borer may modify the expression of resistance and give an understanding of discrepancies in the results of different experiments. They also have laid the basis for later research.

Preference and nonpreference.—There have been relatively few studies of the attraction or repulsion of insects to or from plants from a distance, where these studies involved resistant and susceptible varieties. It must be emphasized that the insect may be attracted or repelled by a variety of characters of the plant. If a plant does not possess a specific attractive quality, the reaction of the insect may be as if the plant were not there; however, the insect may find the plant by chance. Such nonpreference may be fairly effective even in the absence of competing plants. Brazzell & Martin (34) studied the number of eggs laid by the pink bollworm on *Gossypium thurberi* in comparison with the number laid on the susceptible cotton variety Deltapine 15, *Gossypium hirsutum.* When the two kinds of plants were confined together in the same cage, 79 per cent of the *G. thurberi* bolls were without eggs while 53 per cent were without eggs when *G. thurberi* was alone in the cage. Dethier (61, 62) has correctly emphasized the importance of chemical senses in host selection, but senses such as those concerned with the perception of surfaces [Callahan (42); Ishii (96); Williams (194)] or color Moericke (128)] may also be of importance.

Tolerance.—The basis of tolerance as a component of resistance also has been little studied. Perhaps lack of study of tolerance is because it is difficult to analyze, involving the general vigor of the plant [Smith & Harris (172)] and the ability to repair wounds [Bloch (31)]. Tolerance is also more easily modified by the conditions under which plants grow. Carter (44) has given an excellent review of the injuries caused by insect toxins. Toxins are present in the secretions of such plant sucking insects as mirids and some aphids. Chatters & Schlehuber (47) analyzed the differences in injuries done to the leaves of resistant and susceptible small grains by the greenbug.

Antibiosis.—About a half dozen different effects, some of them obviously related, result from the feeding of insects on resistant plants [Painter (137)]. These include: death of the insect often during the first instar, abnormal length of life, reduction in food reserves sometimes followed by unsuccessful hibernation, smaller size, decreased fecundity, and frequently

restlessness and other behavior peculiarities. Four possible physiological explanations were suggested: (*a*) the deleterious effects of specific chemicals including toxins; (*b*) the lack of specific food materials in parts of plants eaten; (*c*) differences in quantities of food present; and (*d*) food materials present but for some reason not available to the insect. To these should be added (*e*), the presence of materials so repellent that the insects will not eat the plant even though the plant would apparently support life. Insects caged on such resistant plants virtually starve to death. The few recent analyses of the basis for resistance in varieties or species, appear to be concerned with explanations (*a*) and (*e*) [Beck (25); Kuhn & Löw (104)]. It frequently is difficult to separate those two explanations experimentally, especially when first instars are involved or under circumstances that seem to indicate that the same substance may be both repellent and toxic. Most examples of resistance involving high insect mortality may turn out to be concerned with explanations (*a*) and (*e*).

Lower levels of resistance, such as those involving smaller size and lowered fecundity, appear to be the result of nutritional disturbances. Examples of such levels of resistance are the differences in size of the southwestern corn borer when reared on different teosinte plants [Burkhardt & Painter (40)] and some of the differences in size and fecundity that have been found in the study of legume aphids [Peters (147)]. Such nutritional disturbances may involve quantitive or qualitative differences in food or they also may concern the presence of antivitamins or antimetabolites. Fraenkel (76) cited analyses of whole leaves and whole plants as evidence that they should be generally nutritionally satisfactory to insects. This may be quite true but few insects eat whole plants or even whole leaves of plants such as were analyzed. This is especially true of the first instars of insects when antibiosis effects are most evident. It is fairly well known that different species of aphids, leafhoppers, and thrips, for example, confine their attacks primarily to such individual tissues as the phloem, mesophyll, or epidermis. It would be best to confine analyses to the plant part attacked by a particular insect in studies of possible nutritional differences of plant varieties. Beck (23) has reviewed several differences in the known nutritional requirements of various insect species.

The nutrition of green-leaf-feeding insects has not advanced far beyond the point discussed earlier in connection with resistance [Painter (137)]. Pertinent information is reviewed by Lipke & Fraenkel (113) and by Friend in this volume. Not enough emphasis has been placed on the use of resistant varieties, particularly resistant and susceptible isogenic pairs, as tools in the study of insect nutrition. A few studies connecting nutrition with resistance may be mentioned. Auclair & Maltais (15) and Maltais (122) found that, with one exception, the levels of amino acids were lower in peas resistant to the pea aphid than in susceptible peas. Ishii (96) gave some evidence that certain pentosans hindered the growth of larvae of the cowpea weevil. Lipke & Fraenkel (113) questioned the evidence; perhaps this example belongs in

the group of explanation which includes deleterious substances. Plank (151) and Plank & Hagerman (152) found that the infestation of powder post beetles, (*Dinoderus minutus* (Fabricius), on bamboo was related to the amount of starch present. This occurred in differences resulting both from different plant ages and from different species. Stalks with the most starch were the most heavily attacked. It is not clear in this case whether the differences should be classified as antibiosis or preference.

Considerable research has been done in a number of places on the resistance of species of the genus *Solanum* to the Colorado potato bettle. Sometimes it has involved studies on the basis of resistance. Several reviews or papers carrying good bibliographies have been published [Buhr (36); Bukasov & Lebedeva (38); Chauvin (48); Chinn (53); Goerletter (79); Grison (82); Kuhn & Löw (105); Torka (184, 185)]. The earlier literature on resistance and information on some of the species of *Solanum* was reviewed by Painter (137). *Solanum demissum*, *S. chacoense*, *S. Commersonii*, *S. jamesii* and a few other species have served as sources of resistance. Bukasov & Lebedeva (38) record the presence of resistance in other species including *S. gibberulosum*, *S. horovitzii*, *S. bergeri*, *S. depexum*, *S. schreiteri* and *S. punae*, as well as other species in the groups *Acaulia*, *Cardiophylla* and *Glabrescentia*. In some plants of *S. bergeri* the beetles ate only the petioles and stems but not the leaf blade. Kuhn and co-workers [Kuhn & Guahe (103); Kuhn & Löw (104)] identified a material, demissine, or solanine d ($C_{50}H_{83}O_{29}N$) which, when painted in a gelatin solution on *S. tuberosum* leaves or infiltrated into such leaves, protected the leaves from Colorado potato beetle larvae. Thus this substance presumably acts as a repellent so strong that larvae eat little of the leaves containing it. It is apparently still not certain if demissine is also toxic. There are a number of species of *Solanum* that are resistant but do not contain demissine [Boczkowska (32); Bukasov (37); Bukasov & Lebedeva (38); Langenbuch (110, 111)]. In tomatoes the substance tomatine is apparently the repellent that is present [Kuhn *et al.* (106)]. Three chaconins have been isolated from various *Solanum* species and are especially abundant in *S. chacoense* [Kuhn & Löw (105)] but these authors do not consider the amount present sufficient to explain the resistance evident in this species. Schaper (165) found that when Colorado potato beetles were fed on resistant hybrids there resulted a partial or complete suppression of the egg laying capacity, while the feeding on some susceptible hybrids had no effect on the larvae but reduced the fecundity of the adults produced. Thus, in the genus *Solanum* several physiologically active substances may be involved in the basis of resistance.

Important studies have been made on the basis of resistance to the European corn borer in corn. Before about 1951 little information on the chemical basis of resistance to the European corn borer was available. This gap is beginning to be filled in successfully by studies of Beck and his co-workers [Beck (19 to 25); Beck & Lilly (26); Beck *et al.* (27); Beck & Stauffer (28); Loomis (116); Loomis *et al.* (117); Smissman *et al.* (170)]. The account which

follows is taken from these papers, supplemented by abstracts distributed for Beck at the 1957 meeting of the North Central Branch, Entomological Society of America. The basic factors underlying orientation and feeding behavior of young larvae in the whorl include negative phototaxis, positive thigmotaxis, and positive saccarotrophic responses which result in the larvae reaching the area of highest sugar concentration in the whorl. The nutritional deficiences that might be present in the corn tissues were not considered sufficient to account for high larval mortality on young seedlings. Requirements for proteins and for sugar change during larval life. The responses of the larvae tend to bring them in contact with tissues that are nutritionally most satisfactory for the larval stage concerned.

A useful contribution to these nutritional studies has been the development of an artificial, but not completely synthetic, diet that was satisfactory enough to permit the use of various substitutions in a study of constituent parts of resistant and susceptible varieties in different stages of their growth. A "leaf factor" necessary for normal larval growth was found in corn leaves and tassels and to a less extent in certain other tissues. This corn "leaf factor" is apparently a food requirement but not a feeding stimulant. Its chemical identity is so far unknown.

Beck and co-workers also found a group of toxic substances, each differing in distribution and concentrations in different tissues (whorl, leaf sheath internode, etc.) in different inbreds. The inbreds chiefly studied were W201D, resistant; and W204, susceptible. Resistance factor A, which has been characterized as 6-methoxy-2(3)-benzoxazolinone, has been isolated and synthesized. Two other factors, B and C, have been isolated but not yet identified. All are completely absent from tassels of all varieties studied. One or more factors may be present in certain tissues but replaced by another factor in different tissues. It was shown that the addition of glucose suppressed the effects of A but not B. This explains the observed relationship of sugars to resistance. The growth inhibition of resistance factor A was greatest during first larval instars and progressively less as the larvae matured. Thus, the variables in the complex bases of resistance of corn to the European corn borer at present include (*a*) the morphology of the plant, (*b*) the stage of growth of larvae and, (*c*) of the plant, (*d*) the concentration of sugar in tissues, and (*e*) the relative concentration of the three different resistance factors in the various tissues. This analysis does not, so far, include the chemical basis in nonpreference for oviposition nor does it include the basis of tolerance, both of which concern the difference between resistant and susceptible strains as seen and measured in the field. One is tempted to speculate on the possible relations between the three or four genetic factors concerned in borer resistance and the resistance factors and sugar distribution studied by Beck.

Perhaps some light is thrown on the relation of plant hairiness to insect resistance by the work of Fukuda (77), who, in studying the relation of the cotton leafhopper, *Chlorita biguttula* Ishida, to egg plant varieties, found that the length and density of hairs on resistant varieties prevented the first instar nymphs from feeding successfully because the proboscis appeared

to be too short. Apparently other factors also were part of the basis of resistance.

Some of the ecological factors that influence the expression of resistance are reviewed by Painter (139). These include particularly the effect of soil constituents by way of the plant on the expression of resistance. This subject is also discussed by Lipke & Fraenkel (113). There seems no reason to change the original statement that "each species of insect and often each host-plant species or variety constitutes a separate problem. Probably also, each different type of soil constitutes a separate problem," [Painter (139)]. In an interesting recent study, Tanada & Holdaway (179) found that the tomato bug, *Cyrtopeltis modestus* (Distant), tended to show considerable preference for plants grown on soil containing high rates of nitrogen fertilizer.

Biotypes.—The presence of biological strains of insects constitute an important feature of the environment that may modify the expression of resistance. Such biotypes may occupy definite geographic areas as has been reported for those of the hessian fly. Ankersmit (5) found a strain of *Phaedonia inclusa* Stål feeding on soybeans in Java where in other areas most of the population of this beetle fed on native legumes. Callenbach (43) in Montana found no evidence of the development of biotypes in the wheat stem sawfly as related to the resistant variety Rescue. Turner (186) reported that the hybrid Oh51A×Oh43, which is resistant to European corn borer in the Middle West did not show low larval survival in Connecticut and (187) considered the small differences found to result from synchronization of stage of borer and stage of development of the corn. As previously indicated [Painter (137)] such differences may also result from the presence of a different biotype. Howitt & Painter (94) reported the presence of biotypes in the corn leaf aphid in relation to resistant varieties in sorghum. Gallun (78) has continued the study of biotypes of hessian fly in Indiana where a laboratory strain has been selected from the general population present. This strain (B) is able to develop on susceptible wheats and also on any resistant variety carrying the gene H_3, but not on other resistant wheats. Gallun has succeeded in isolating another race (C) able to develop on resistant wheats carrying the genetic factors from the Durum P.I. 94587 but not on wheat carrying the resistant gene H_3 or other factors for resistance. A third race (D) has been developed from segregates from the cross between the races B and C which is able to develop either on wheats carrying resistance factor H_3 or those wheats derived from P.I. 94587. Thus, in hessian fly resistance evidence is developing of the relationship between particular genetic strains of the insect and specific genes for resistance in wheat. Because of this relationship, varieties carrying different genes for resistance provide protection against the development of biotypes. Such varieties are now being tested in yield nurseries at several localities.

Inheritance of Resistance

The search for sources of resistance must precede the study of inheritance of resistance. Typical of such work is that reported for greenbugs by Dahms *et al.* (57), Painter & Peters (144) and Melhus *et al.* (127). In the latter case

resistance to *Diabrotica* spp. in corn was located in strains from near the area of origin of both the insect and the crop. Some researches have concerned the inheritance of physical factors associated with insect resistance. Examples of such studies are those by McNeal (121) on wheat stem sawfly as related to stem solidness and Knight (101) on hairiness of cotton as related to leafhopper resistance. Sikka & Singh (167) found that the resistance to injury of cotton by leafhoppers was determined by two factors, resistance being dominant over susceptibility. In a study of the resistance of barley to greenbug, Dahms *et al.* (57) found that resistance depended on one or two gene pairs varying with the parents used. Painter & Peters (144) had preliminary evidence of a single factor governing resistance to greenbugs in wheat but detailed studies may show additional factors to be present. Horovitz *et al.* (93) and Rosbaco (159 to 162) have made further studies on the inheritance of resistance to locusts in corn. The most detailed information on the inheritance of resistance is available in studies with the European corn borer and the hessian fly. A group of papers on resistance in corn to the European corn borer [Fleming (75); Ibrahim (95); Loeffel (115); Penny & Dicke (146); Rubis (163); Singh (168)] indicate that a series of two to four major genes are concerned in resistance primarily as determined in the whorl. Certain differences in the results obtained by these investigators are due at least partly, to a difference in the resistant and susceptible plant materials used and to methods of measuring resistance. The recent analysis of the basis of resistance by Beck and co-workers suggests the necessity in the future of defining more closely the kinds of resistance for which inheritance is being measured.

New evidence on the inheritance of resistance to hessian fly in wheat [Allen *et al.* (2); Shands & Cartwright (166); and Suneson & Noble (178)] bring to a total of five the number of genes concerned with resistance. Other sources of resistance which apparently carry additional genes for resistance are known. All of these half dozen or more genetic factors are concerned with the ability of the young larvae to survive on the wheat plant after reaching the normal feeding place.

Concluding Remarks

A valuable beginning has been made in the use of insect resistant plants to control insect populations and damage. A little progress has also been made in understanding the basis of resistance which is proving to be more complex than many have thought it to be. Almost invariably varieties resistant to one insect may be susceptible to another. Omugi barley carries high resistance to greenbug but is very susceptible to corn leaf aphid. Alfalfa plants resistant to the spotted alfalfa aphid often have been susceptible to the pea aphid. Numerous examples of this contrasting relationship have been found amoung the species of legumes studied by Peters (147). The reverse situation is probably fortuitous, for example, where sorghums are resistant to grasshoppers and chinch bugs or certain corn hybrids resistant to the

European corn borer and corn leaf aphid. However, few unsurmountable difficulties have so far been reported in combining resistance to two insects.

Newer techniques in chemical analyses should help in identifying the chemical bases of resistance and, in special cases, give practical help in tracing the genes concerned in insect resistance.

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BIOLOGICAL CONTROL OF INSECT PESTS[1]

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Control of agricultural insect pests by the biological method has made remarkable strides during the past 25 years, and an adequate treatment of the subject necessitates coverage of at least that period rather than the five or ten years to which many other reviews are limited. Many projects are of long duration and there is frequently considerable delay in the publication of final results. The last general review of the subject was that by Sweetman (96). Because of the space limitations, this review will deal only with the utilization of insect parasites and predators in control of crop pests, and the rapidly expanding field of microbial control, wherein disease-producing organisms are utilized for the same purpose, will not be considered here. Likewise, the subject of the effect of chemical control practices upon populations of parasites and predators, which has become of great importance since the advent of DDT and other high toxic chemicals, and the means whereby these harmful effects can be alleviated, will be excluded from consideration.

The very large number of biological-control projects that have been undertaken during the period under review makes it impossible even to list them, and those selected comprise pest species with which the outcome has been highly successful or which demonstrate techniques or phenomena that are of special interest to workers in this field. It is noteworthy that, as in the past, the greatest attention has been given to the scale insects, mealybugs and white flies, and the successes in control have been more numerous with the homopterous pests than with species of other orders.

Unfortunately, detailed reports are not available regarding many important projects, other than a brief statement of the final general outcome. General reviews of the status of biological control in the various countries are available in only a few instances, these being by Clausen (17) for the continental United States, Pemberton (77, 78) for Hawaii, O'Connor (75) for Fiji, Jenkins (59) for Western Australia, Miller *et al.* (69) for New Zealand and Kamal (60) for Egypt.

Results of Biological Control

Coconut moth, Levuana iridescens *Bethune-Baker*.—One of the outstanding examples of biological control of a lepidopterous pest is that on the coconut moth in Fiji, accomplished through the introduction of a tachinid fly, *Ptychomyia remota* Aldrich, and reported upon in detail by Tothill *et al.* (104). Field control of the pest was accomplished in many areas within six months after release of the parasite, and economic control was general throughout

[1] The survey of the literature pertaining to this review was completed in June, 1957.

the Islands within two years. Field releases of insectary-reared material totalled 32,570, mainly parasitized host larvae. Several factors were highly favorable for this successful outcome. The life-cycle of the parasite is very short in relation to that of the host, and the adults have exceptional powers of dispersion, having negotiated in one instance a flight of 12 miles over water. Further, the mild climate of Fiji throughout the year, and the overlapping generations of the host, provide optimum conditions for uninterrupted increase.

A noteworthy feature of this project is that *Ptychomyia*, native to Malaya, is a normal parasite of another genus and species, *Artona catoxantha* Hampson. In the history of biological control, instances of successful utilization of parasites from another host genus are exceedingly rare.

Oriental fruit moth, Grapholitha molesta (*Busck*).—This pest is now attaining worldwide distribution and large-scale efforts in biological control have been undertaken in the United States and other countries. A large number of parasite species were introduced into the United States from Japan and China (50) but only one, *Agathis diversus* (Muesebeck), became established, and that at only a very few points. Greater success was attained through use of a native parasite, *Macrocentrus ancylivorus* Rohwer, which adapted itself to this host. Wide distribution of this parasite resulted in high parasitization in most areas, accompanied by a marked reduction in fruit infestation (119). Similar results are reported from Canada (108). The introduction of *Macrocentrus* into other countries, such as Australia, France, Italy, Argentina, and Brazil have not been effective, possibly because of lack of a suitable alternate host.

Brunson & Allen (12) found that mass releases of *Macrocentrus* at an average rate of 330 per acre in New Jersey, in seasons when the native population was inadequate, resulted in a reduction of approximately one-half in fruit infestation.

Macrocentrus was employed widely in one phase of the unsuccessful attempt to eradicate the oriental fruit moth in California during the early 1940's when more than 48 million were released in infested orchards during a three-year period (35). This was on an inundative basis, the releases often far exceeding in numbers the pest populations in the orchards. Field recoveries were made the season of release, but the parasite failed to become established in that state, though the pest itself has persisted, but at a generally low level, in several areas.

Codling moth, Carpocapsa pomonella (*Linnaeus*).—The attempts to control this pest biologically have centered mainly on the use of the egg parasites, *Trichogramma* spp. Some reductions in fruit infestation are reported for the United States (1) and Spain (106), while in Russia substantial reductions were obtained in orchards having heavy infestations (85), but other tests have been inconclusive. All experiments have involved release of several thousand parasites per tree. In general, the results obtained against fruit insects have not been sufficient in the extent of control or consistency to warrant recommendation for the use of this parasite by growers. Larval para-

sites, mainly *Ascogaster quadridentata* Wesmael and *Mastrus carpocapsae* (Cushman) have been tested in several countries, but without success.

Coconut spike moth, Tirathaba trichogramma *Meyrick*.—An extensive program for the biological control of this pest in Fiji was carried on for a number of years. The details of the importation and colonization program are given by Paine (76), who reports four parasite species from Java as established, the most important being *Apanteles tirathabae* Walker and *Erycia basifulva* Bezzi. The injury by the pest, premature nutfall, was checked, although control was not complete (64).

Oriental moth, Cnidocampa flavescens (*Walker*).—The introduction and establishment of the tachinid fly, *Chaetexorista javana* Brauer & Bergstrom, into Massachusetts resulted in full control of the oriental moth except during seasons following exceptionally cold winters. This example illustrates strikingly the differential effect that may be exerted upon host and parasite by low temperatures. It was found by Dowden (29) that winter temperatures below 0° F. are lethal to the second-instar parasite larvae in the hibernating host prepupae, yet the unparasitized hosts are not affected. A minimum temperature of −19° F. in 1933 resulted in a field parasitization of less than 10 per cent the following season, but the normal high parasitization was regained in following years.

Imported cabbageworm, Pieris rapae (*Linnaeus*).—A substantial reduction in infestations of the cabbageworm, though not consistent field control, is reported from New Zealand by Muggeridge (70). This was accomplished by the pupal parasite, *Pteromalus puparum* (Linnaeus), and field parasitization often approaches 100 per cent.

Sugarcane borer, Diatraea saccharalis (*Fabricius*).—Extensive efforts have been made in many of the countries of the Western Hemisphere to control the sugarcane borer by the biological method. The earlier attempts were in the use of the egg parasite, *Trichogramma minutum* Riley, and reductions of crop loss of 50 per cent are reported by Tucker (105) in Barbados and substantial reductions by Smyth (93) in Peru and Wolcott & Martorell (116) in Puerto Rico. A detailed series of experiments in Louisiana by Jaynes & Bynum (58) involving releases of up to 45,000 *Trichogramma* adults per acre resulted in no benefit whatever. These conflicting results may well be due to differences in climate and cultural practices, cane being an annual crop in Louisiana.

The introduction and establishment of the Cuban fly, *Lixophaga diatraeae* (Townsend), in southern Florida resulted in partial control, the parasitization often amounting to 65 per cent or more, aided in some areas by *Agathis stigmaterus* (Cresson) (83). Climatic conditions, especially unusually cold winters, are adverse to the parasites, so that there is a wide fluctuation in parasitization from season to season, and recolonization is at times necessary. The introduction of *Lixophaga* into St. Kitts in the West Indies resulted in a substantial reduction in borer injury (8).

The Amazon fly, *Metagonistylum minense* Townsend has been very widely colonized and has become established on several islands of the West

Indies, with a considerable degree of control reported on the island of St. Lucia (7).

Larch sawfly, Pristiphora erichsonii (*Hartig*).—The biological control of the larch sawfly in Canada through the introduction of *Mesoleius tenthredinis* Morley from England in 1910–11 was highly successful for a period of years thereafter, but a decline in effectiveness of the parasite was noted in Manitoba beginning about 1940. A detailed study by Muldrew (71) of the factors responsible for this situation revealed that, in Manitoba and Saskatchewan, the pest has developed a pronounced immunity to successful parasitization by *Mesoleius*. Dissections of parasitized larvae showed that more than 90 per cent were able to destroy the embryo before hatching, this being accomplished by phagocytic action resulting in encapsulation of the developing egg. No evidence of immunity was found in material from British Columbia, but the parasite has been established in that province only since 1934–36. Recent observations by Drooz (31) in New York reveal a fairly high parasitization, with no evidence of physiological resistance, so that the phenomenon is at present limited to the areas of earliest establishment.

This situation has serious implications in biological control of crop pests, though fortunately it appears to be an isolated case, and a comparable loss in field effectiveness of a parasite species has not heretofore been recorded. One wonders if this development in the *Pristiphora-Mesoleius* relationship is a selection process whereby the susceptible elements in the population have been progressively eliminated and is therefore analagous to the development of resistance to insecticides by many pest insects.

European spruce sawfly, Diprion hercyniae (*Hartig*).—The biological control of this pest in eastern Canada has been one of the largest scale projects to date. During the 1930's and continuing into the following years, a large series of parasites was imported from Europe and many were successfully established (4, 80). Special attention was given to the pupal parasite, *Dahlbominus fuscipennis* (Zetterstedt), of which hundreds of millions were released each year. Many of these parasites were later released in infested states, especially Maine, in the United States and *Dahlbominus* became established (30). In the early 1940's an epidemic outbreak of a virus disease of the larvae developed and in a few years greatly reduced the infestations in all areas. The final outcome of the parasite release program was for that reason obscured. Unfortunately, an over-all account of this project has not yet been published, though many articles have dealt with individual elements in the parasite complex.

Coconut leaf-mining beetle, Promecotheca reichei *Baly*.—The work on the coconut leaf-mining beetle in Fiji is an outstanding but rare example of successful biological control of an endemic insect pest. Originally an economic balance had been maintained between the pest and its natural enemies, but this balance was upset by the accidental introduction of a predacious mite, *Pediculoides ventricosus* Newport, into the complex. This mite caused the periodic elimination of all developmental stages of the host and thus evened

the successive generations of the beetle in contrast to the overlapping of the generations so essential to the continued effectiveness of the native parasites. Taylor's (98) detailed account of this problem and its solution presents several points of special interest.

Before undertaking foreign exploration for effective natural enemies, the situation was reviewed and an analysis made of the attributes required of the parasites to accomplish control under the changed conditions mentioned above. A search was then made in Java for parasites fulfilling those requirements. *Pleurotropis parvulus* Ferriere, an internal parasite of all of the larval stages and of the pupa as well, the normal hosts of which are other species of *Promocotheca* in Java, appeared to meet all requirements. Its introduction into Fiji and the early release of a total of 25,900 adults resulted in complete economic control in less than one year. Other successful efforts for the control of hispid leaf-miners have been on *Brontispa frogatti selebensis* Gestro by *Tetrastichodes brontispae* Ferriere, a larval-pupal parasite, in Celebes (3) and on *Brontispa mariana* Spaeth in the Palau Islands by the same parasite (26, 62).

Eucalyptus snout weevil, Gonipterus scutellatus *Gyllenhal.*—This snout weevil is native to Australia and has spread to many countries in which eucalyptus is grown for timber purposes. It became exceedingly destructive in South Africa, and biological control efforts, beginning in 1926, resulted in the importation from Australia in that year and the establishment of an egg parasite, *Anaphoidea nitens* Girault. The recent detailed account by Tooke (103) of progress on this project, covering the period from 1926 to 1950, with its extended consideration of all factors bearing upon reproduction and increase of host and parasite, is one of the outstanding contributions to biological control in recent years. Too often, successes are reported only briefly, without details as to production techniques, field observations, etc.

The parasite brought about rapid and full economic control in all of southwestern and southern Cape Province and generally in most other areas below 4000 ft. elevation. Mild winters with mean minimum temperatures not below 48° F., with winter or all-year rainfall, were found to be most favorable for parasite effectiveness. In highland areas, such as occur in the Transvaal and Natal, the cold and dry winters retarded control, as both conditions prevent host oviposition for several months in the spring and thus shorten the period of activity of the parasite, and the populations fluctuate accordingly. Overall, the parasite has shown its adaptability to an unusually wide geographic and climatic range.

The host has 2 to $2\frac{1}{2}$ generations each year and each female deposits 180 to 270 eggs, whereas the parasite has 5 to 6 generations and deposits 25 to 50 eggs, thus permitting very rapid build-up. Dispersion of the parasite is rapid, instances having been noted of spread of more than 20 miles in three months and 100 miles in a single season. Effective control was accomplished on 63 of 65 species of eucalyptus grown in South Africa.

This is one of the exceedingly few instances of a pest insect being con-

trolled by an egg parasite alone. It has generally been assumed that egg parasites represent a mortality factor of relatively minor importance, as they are seldom able to destroy a sufficiently high portion of the host eggs to have a dominant influence on the host population.

Since its introduction into South Africa in 1926, *A. nitens* has been introduced into and established in Argentina, Kenya, Madagascar, Mauritius, New Zealand, and Rhodesia, in several of which, notably New Zealand (69), Madagascar (49), and Mauritius (114), it has been equally as effective as in South Africa.

Fruit flies (*Tephritidae*).—Investigations on the biological control of fruit flies of the family Tephritidae have been conducted in several countries, with the major efforts centered on the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann); the oriental fruit fly, *Dacus dorsalis* Hendel; and the melon fly, *Dacus cucurbitae* Coquillett, in the Hawaiian Islands (18). The early work on the Mediterranean fruit fly during 1912–16 resulted in the establishment of five parasite species, of which *Opius tryoni* (Cameron) from Australia was the most effective, and brought about a substantial reduction in infestations in certain fruits, especially coffee.

Opius fletcheri Silvestri, the parasite of the melon fly imported from India, has not had an appreciable influence on the host infestations, and recent studies by Newell *et al.* (72) and Nishida (73) reveal that its activities, as represented by the percentage of parasitization are much reduced during the summer months. Fruit infestation is now higher and parasitization lower than reported by Willard (113) for the period shortly after introduction of the parasite.

The appearance of the oriental fruit fly in Hawaii in 1946 led to a very large parasite importation program, in the course of which 4,246,000 puparia of that and about 60 other species of the family were imported for parasite rearing (18). Eleven species and varieties of parasites are known to be established and field parasitization now averages 70 to 75 per cent. Field infestations have been reduced substantially, though chemical control methods still need to be employed in commercial orchards and gardens. The changing relative status of the three major parasite species, as reported by van den Bosch & Haramoto (107), is of special interest. *Opius longicaudatus malaiensis* Fullaway, the first established, very quickly attained a high rate of parasitization, but was superseded the following year by *O. vandenboschi* Fullaway. The latter in turn was replaced a year later by the egg-larval parasite, *O. oophilus* Silvestri. This last species has been, virtually alone, responsible for the continued high parasitization since 1950. Its effectiveness is enhanced by a fungous disease of the host eggs that is transmitted by the parasite females when ovipositing.

Mealybugs (*Pseudococcidae*).—The mealybugs as a group appear to be especially amenable to biological control. The early introduction of *Cryptolaemus montrouzieri* Mulsant and *Leptomastidea abnormis* (Girault) into California led to partial control of the citrus mealybug, *Planococcus citri* (Risso),

and later, in 1928, the complete control of the citrophilus mealybug, *Pseudococcus gahani* Green, was achieved by *Coccophagus gurneyi* Compere and *Tetracnemus pretiosus* Timberlake (20). So effective were these latter parasites that it has become difficult to find even a single specimen of the host in the citrus orchards. The long-tailed mealybug, *Pseudococcus adonidum* (Linnaeus), on avocado was likewise controlled in that state by *Anarhopus sydneyensis* Timberlake and *Tetracnemus peregrinus* Timberlake, imported from Australia (41).

The Comstock mealybug, *Pseudococcus comstocki* (Kuwana), a pest of several deciduous fruits, has spread from Japan to many parts of the world. Its principal parasites, *Allotropa burrelli* Muesebeck, *Pseudaphycus malinus* Gahan, and *Clausenia purpurea* Ishii, the first two imported into the United States in 1939–41, have been effective in bringing about economic control in practically all states, typical being the outcome in Ohio as reported by Cutright (21). Published accounts for other states are not yet available. According to Rivnay (82), a substantial reduction of what is questionably considered to be *P. comstocki* on citrus in Israel has resulted from the importation and establishment of *C. purpurea*.

An extended program for the biological control of the coffee mealybug, *Planococcus kenyae* Le Pelley, was undertaken in Kenya from 1925 onwards, though large-scale efforts were conducted by Le Pelley (63) during 1936 and following years. Because of uncertainty as to the identity of the pest, the search for its natural enemies extended to many tropical and subtropical regions of the world, but effective species adapted to it were found only in nearby Uganda and Tanganyika. *Anagyrus kivuensis* Compere proved to be the most effective, aided in some localities by *Anagyrus* sp. and *Pauridea peregrina* Timberlake. Full economic control was not attained in all infested areas, though substantial reductions in infestations, crop losses, and cost of treatment were brought about.

A large-scale effort has been under way since 1948 on the Gold Coast of Africa for the biological control of *Pseudococcus njalensis* Laing, and a large series of parasites has been imported from many parts of the world (110). This project is of particular interest because the objective is control of the swollen shoot disease of cacao, a virus disease of which the mealybug is the vector. The normal population of the mealybug is low, as compared with infestations of the more common species on citrus and deciduous fruit trees in other countries, and the population needs to be reduced to such an extremely low level to provide control of the disease that the problem becomes exceedingly difficult. The chance of success is consequently greatly reduced.

Citrus blackfly, Aleurocanthus woglumi *Ashby, and other Aleyrodidae.*—The citrus blackfly, native to tropical Asia, has become a serious pest of citrus and other trees in tropical and subtropical America since its discovery in Jamaica in 1913. One parasite, *Eretmocerus serius* Silvestri, and a predator, *Catana clauseni* Chapin, both from the Malayan region, were imported and established in Cuba (19). Full economic control was accomplished very

quickly, not only in Cuba but in other West Indian Islands, and the Panama Canal Zone and Costa Rica as well. This was through *Eretmocerus* alone, though *Catana* demonstrated a capacity to reduce heavy infestations very quickly. It is unable to persist in light infestations, however, and, therefore, has little value in holding infestations at a low level. Its highly specialized habits, limiting feeding to the eggs and first-instar larvae, preclude its maintaining full control without the aid of other natural enemies.

After the finding of the citrus blackfly in Mexico, a cooperative project between the agricultural organizations of that country and the United States was set up to undertake biological control. *Eretmocerus serius* was imported and established but proved to be ineffective because of adverse climatic conditions. Additional species of parasites were then imported from India and Pakistan during 1948–50 and became established, these being *Amitus hesperidum* Silvestri, *Prospaltella clypealis* Silvestri, *Prospaltella opulenta* Silvestri, and *Prospaltella smithi* Silvestri. The distribution program has been the largest of any similar project, hundreds of millions of these parasites being colonized annually. According to H. D. Smith (89), economic control has been achieved in practically all parts of the country, with the exception of small areas on the West Coast. *Amitus* has been most generally effective, while the several species of *Prospaltella* have been able to control the pest under special and limited conditions.

A related blackfly species, *Aleurocanthus spiniferus* Quaintance, was brought under control in Japan by *Prospaltella smithi* (61), and in Guam by *Amitus hesperidum* and *P. smithi* (79).

The methods originally developed by Speyer (95) for the production of the greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood), and its parasite, *Encarsia formosa* Gahan, have permitted effective and economical biological control of the pest in greenhouses. The whitefly is produced on a mixed stock of tomato and tobacco. The latter plant, being unattractive to the parasite, maintains a high whitefly population from which the tomato plants are continuously infested, and the parasitized whiteflies from that plant are utilized for distribution. Effective control of the pest has been reported in England, Australia (102), Canada (66), and Belgium.

Coconut scales, Aspidiotus destructor *Signoret and others*.—The most important of the scale insects attacking coconut in many tropical areas is *A. destructor*, and a detailed account of the highly successful efforts to control it biologically in Fiji has been presented by Taylor (97). A considerable number of parasite and predator species were imported from Java and Trinidad and several of the predator species became established. A single coccinellid species, *Cryptognatha nodiceps* Marshall, was highly effective and very quickly brought the pest under full economic control in all islands of the group.

C. nodiceps is considered to have several qualities that contribute to an exceptional degree to field effectiveness, among them being its specialized feeding habit in both the larval and adult stages, long adult life, a high re-

productive capacity, and remarkable powers of dispersion. Other factors contributed to the high degree of control attained, one of the most important being the gregarious or colonial habit of the host, which provides adequate food for the immature stages of the beetle, with a minimum of searching required, and second, and perhaps most important, the mild climate of Fiji which permits reproduction throughout the year.

The success with *Cryptognatha* in Fiji led Taylor to state that "Parasites have invariably failed as complete and permanent controls for scales" and "as a general rule it is desirable to seek predators rather than parasites for the control of a scale which, like *A. destructor*, does its damage only by severe outbreaks." It is unquestionably true that the highly specialized predators, such as *Cryptognatha*, *Catana*, and *Rodolia*, are very valuable, but the number of such species is small and the great majority of scale insects do not have predator enemies of similar capacity. The successes with parasites of scale insects, mealybugs and whiteflies have now greatly exceeded in number those by predators alone.

Other scale insects are destructive to coconut in various parts of the world, and in the Seychelle Islands the two most important species are *Pinnaspis buxi* (Bouché) and *Ischnaspis longirostris* (Signoret). A series of predators was imported during 1936–38, of which the most effective proved to be *Chilocorus nigritus* (Fabricius) from India. A survey of the field situation by Vesey-Fitzgerald (109) in 1952 revealed that *C. nigritus* had reduced very substantially the infestations in the Islands, resulting in a marked increase in nut production.

California red scale, Aonidiella aurantii (*Maskell*).—Work on the biological control of the California red scale, a destructive pest of citrus, has been under way in California for sixty years, yet it was only after the introduction of *Aphytis lingnanensis* Compere from South China in 1949 that appreciable results in control have been attained. This outcome has been limited, however, to the coastal area. Periodic releases, totalling 100,000 or more per acre each year, have yielded economic control in several intermediate climatic areas where the natural population was ineffective (25). The red scale race of *Prospaltella perniciosi* Tower, obtained from Formosa, shows considerable promise.

The closely related yellow scale, *A. citrina* (Coquillett), is adequately controlled in southern California by the Japanese race of *Comperiella bifasciata* Howard, obtained from *Aonidiella* on *Podocarpus*, but is ineffective against the pest in the San Joaquin Valley (44).

Juniper scales, Carulaspis visci (*Schrank*) and Lepidosaphes newsteadi *Šulc.*—An extensive program for the biological control of these two destructive pests of Bermuda cedar, *Juniperus bermudiana*, was undertaken in 1947 by the Commonwealth Institute of Biological Control. Thompson (101) reports that of 30 to 35 species of parasites and predators introduced, only two became well established, these being *Lindorus lophantae* (Blaisdell) and *Microweisea suturalis* Schwarz. In spite of high parasitization by *Aspidioti-*

phagus and heavy feeding by the coccinellids, the program was unsuccessful because of the extremely lethal effects of even small populations of scale upon the trees.

Olive scale, Parlatoria oleae (*Colvée*).—The biological control program on the olive scale in California serves to illustrate several problems that may confront workers in this field. Stocks of *Aphytis maculicornis* (Masi) imported in 1951 from the area extending from India through the Middle East to the Mediterranean proved to be indistinguishable morphologically, yet studies by Hafez & Doutt (51) revealed the existence among them of three races or sibling species that have been designated as the Indian, Persian, and Spanish forms, and which show distinct biological differences. Under field conditions in California the Persian form has proven to be most effective. The results obtained in this study emphasize once again the need for obtaining stocks of each parasite species from all parts of its geographic range, rather than from only a single source.

Doutt (27) reports that *Aphytis* increased rapidly in the experimental orchards in which it was released and often attains a parasitization of 90 per cent or more of the spring brood of scales. Attack upon the summer generation is always low, very seldom exceeding 20 per cent. The general scale population on the trees in the years following parasite release was substantially less than 10 per cent of that occurring previously, so that, on the basis of ordinary criteria, the trees were commercially clean. It developed later, however, that the few remaining scales of the second generation were largely concentrated on the fruit. Thus the fruit injury, which is the main cause of loss from this pest, is reduced very much less than the reduction in numbers of the pest itself.

Fig scale, Lepidosaphes ficus (*Signoret*).—The apparently successful control of this pest of figs and other plants is another instance of the occurrence of host-determined races of a parasite species. The one involved, *Aphytis mytilaspidis* (LeBaron), occurs as a parasite of *Lepidosaphes* throughout the United States, but in California it parasitizes only a very small proportion of the fig scales. The importation and colonization of stocks of this parasite from fig scale in Italy resulted in high field parasitization and apparent economic control at the release sites (28, 48, 56).

Pustule scale, Asterolecanium pustulans *Cockerell*.—This pest of certain shade and forest trees in Puerto Rico was so completely controlled by the introduced *Chilocorus cacti* Linnaeus that specimens of the scale could not be found over a period of 12 years after general establishment of the predator, though it has since been taken in small numbers (115).

Black scale, Saissetia oleae (*Bernard*).—Prolonged efforts to find effective natural enemies for the control of the black scale in California finally resulted in partial success when *Aphycus helvolus* Compere was obtained from South Africa in 1937 (90). This parasite has proven to be most effective in the coastal areas where the "uneven hatch" condition of the host prevails and where winter temperatures are milder than in the interior valleys. Protracted

cool periods in these valleys during the winter are often followed by heavy scale infestations. While full or partial economic control of the scale on citrus is effected by *Aphycus* under favorable conditions, yet it is noteworthy that in no instance has the parasite been effective against this pest on olives in the San Joaquin and Sacramento Valleys. A byproduct of the extensive distribution of *Aphycus* against the black scale was its complete suppression of a related species, *Saissetia nigra* (Nietner), a pest of shade and ornamental trees in southern California.

The introduction of the several black scale parasites into other countries has given variable results. In southern Peru, for example, where *S. oleae* was a serious pest on olive, the infestations were brought under control by *Aphycus lounsburyi* Howard, *Scutellista cyanea* Motschulsky and *Lecaniobius utilis* Compere (6). This outcome must be attributed mainly to *Aphycus* as, on the basis of observations in California, the egg predators, even when very abundant, contribute very little to reduction of the infestations.

Red wax scale, Ceroplastes rubens *Maskell*.—The red wax scale became one of the most destructive pests of citrus and other fruit trees and shrubs in Japan following its appearance in that country about sixty years ago. Several parasites were known to attack it, though in very small numbers, but this situation changed rapidly after 1946, when Yasumatsu (117) found that a highly effective parasite had appeared in Fukuoka Prefecture and was spreading rapidly. It was first determined as *Anicetus ceroplastis* Ishii but later described as a new species, *A. beneficus* Ishii & Yasumatsu. Following this discovery the parasite was reared in large numbers and widely distributed, and economic control has already been attained in many areas of Kyushu and Honshu.

There are several possible explanations of the sudden appearance of *A. beneficus* in Japan, and Yasumatsu (118) expresses the belief that it may have arisen by mutation from the native *A. ceroplastis*. This explanation, of course, cannot arbitrarily be excluded, though such a development has not heretofore been observed within the parasite complex of any other pest insect. A second possible explanation of the situation is that *A. beneficus* is a recent accidental introduction from abroad, presumably from China, but this too is at present questionable inasmuch as the species has not thus far been represented in any of the numerous collections of *Anicetus* from the Asiatic mainland.

Cyclamen mite, Steneotarsonemus pallidus (*Banks*).—The biological control of phytophagous mites presents exceptional difficulties and, on the basis of our present knowledge, the prospects cannot be considered encouraging. Some progress has been made on the cyclamen mite problem on strawberries in California, where Huffaker & Kennett (57) have demonstrated a method whereby control may be accomplished through manipulation of native predaceous mites, *Typhlodromus cucumeris* Oudemans and *Typhlodromus reticulatus* Oudemans. Old fields normally have high populations of the predator and distribution of clippings from normal winter pruning into in-

fested fields gave good control. It is suggested that equilibrium of pest and predator may be attained early in each planting if deliberately stocked with both during the first growing season.

Research Relating to Biological Control

Mass production of parasites and predators.—The work and cost involved in the insectary rearing of parasites and predators employed in many biological-control programs has been very greatly reduced, in many instances, through the development of mass production methods. When practicable, it permits production to meet any colonization program in a minimum of time and also, at an economically practicable figure, in numbers sufficient for periodic or inundative release programs against certain types of pests. In some cases, where the host stage to be parasitized is inactive, such as the eggs of the gypsy moth and those of the range caterpillar, or the cocoons of the European spruce sawfly, the host material can be collected in the field in virtually unlimited quantities, and the rearing of parasites presents no particular problem. It is more difficult, however, when sap feeders, such as scale insects and mealybugs, fruit feeders, such as the fruit flies and codling moth, and stem borers are involved. Obviously, it would be economically impracticable to produce the required number on the normal food plant of such pest insects. The general subject of culture of entomophagous insects has recently been reviewed by Flanders (45). He concludes (47) that in most production programs the increase to be expected under any economical method is about equal to the average number of eggs deposited per day by the parasite female.

In the mass culture of entomophagous insects the main problem usually is concerned not with the parasites or predators themselves but with the host insects. It may be solved by (*a*) the production of the host on plant parts, such as melons, tubers, etc., that are not normally infested in the field; (*b*) the utilization of a factitious host (86) amenable to rearing on such plant parts, that is acceptable to the parasite or predator; and (*c*) the development of artificial food media for host or parasite.

Potato sprouts have proven to be suitable for the production of various mealybugs (91) and the black scale (38) while the tubers themselves are excellent for the production of California red scale (46), latania scale, and many other diaspine scale insects (43). The fruits of various Cucurbitae, especially squash and citron, serve for the production of California red scale (39), San Jose scale (40), oleander scale, and many others. Ripe oranges were found to be satisfactory for the production of six-spotted mites (33).

Examples of factitious hosts utilized in parasite rearing programs are the Angoumois grain moth and other stored grain pests produced in corn or wheat for the production of the egg parasites, *Trichogramma* spp. (36, 94), the Mediterranean flour moth for rearing of *Chelonus* and *Bracon* species (10, 74), the potato tuberworm in potatoes for the production of *Macrocentrus ancylivorus* (35), a parasite of the oriental fruit moth, and the eggs and larvae of the tuberworm for production of the predator, *Chrysopa*

plorabunda Fitch (32). Many of the parasites of dipterous puparia may be readily reared in puparia of *Drosophila*, house flies, blow flies, etc.

The costs of mass production of hosts and parasites may be greatly reduced through measures developed to obtain maximum reproductivity of the species involved. Synthetic foods for the adults may serve this purpose. It was found by Hagen (52) that egg deposition of *Chrysopa plorabunda* was greatly increased by adding an enzymatic hydrolysate of brewer's yeast to the honey solution fed to the adults. With host insects, Hagen & Finney (53) report that fecundity of the oriental fruit fly was very greatly increased through the use of the same food supplement.

The formulation of synthetic food media for the parasites themselves, as a substitute for the normal insect host, has intrigued many workers in the past, though little research was done on the problem. The complex nutritional requirements of both endo- and ecto-parasites, as well as the changing physical conditions required as development progresses from egg to pupa, seemed to present insurmountable difficulties. The parasitic species of the dipterous family Sarcophagidae, present possibly the simplest problem, and it was one of these, *Pseudosarcophaga affinis* (Fallén), parasitic in the spruce budworm, *Choristoneura fumiferana* (Clemens), that was the subject of study by House & Traer (55). It was found that a food medium consisting of pork liver and fish was fully acceptable to the larvae and that a much higher proportion reached maturity on this medium than on the normal insect host. This permitted year-round production of the parasite in any desired quantity, a great advantage when dealing with a univoltine host. House's later work on this same parasite has dealt with a wide range of essential nutrients.

The development of synthetic food media for the host insects has shown considerable promise. Ripley *et al.* (81) found that the false codling moth, *Argyroploce leucotreta* Meyrick, would develop and reproduce readily on a preparation of oatmeal porridge lightly infected with the mold *Mucor hiemalis* Wehmer. In Hawaii, enormous numbers of the oriental and other fruit flies were produced on a medium of blended fresh squash fortified with additional essential nutritive factors (67). Later modification of this method provided for use of fresh carrot (34) and then of commercially available dehydrated carrot (13), which permits of year-round production independent of uncertain supplies of the fresh product.

Various means may be employed to replace the laborious rearing of host material and to insure an ample supply throughout the production program. In the rearing of the aphid-feeding coccinellid, *Hippodamia convergens* Guérin, Haug (54) found that this could be readily accomplished throughout the year by the use of frozen aphids. The species used was the poplar petiole gall aphid, *Pemphigus populi-transversus* Riley. The poplar galls containing the aphids were stored at -21 to $-25°$ C. and remained in good condition for many months. For storage purposes this aphid was more satisfactory than those occurring on open foliage because of the greater ease of handling of the galls containing them and less rapid decomposition and desiccation after removal from storage.

Devices for the automatic collection of host or parasite serve to reduce the cost of mass production programs. Examples are the units developed by Spencer *et al.* (94) for rearing and collecting adults of the Angoumois grain moth and the trap described by Bedford (5) for collecting *Chelonus texanus* Cresson in the rearing rooms. The latter method utilizes two light sources, the first being daylight fluorescent tubes behind a landing screen, from which surface the parasites are then attracted to natural daylight into suitable containers.

Biological studies.—A knowledge of the biology and habits of the entomophagous species (15) being utilized in biological control is obviously of value, though not always essential, in biological control programs. Occasionally, however, such knowledge provides the key to success of an entire program. This was strikingly illustrated by the discovery by Flanders (37) of the phenomenon of sex differentiation in the host relations of a series of *Coccophagus* species parasitic in scale insects, wherein the females develop as primary parasites and the males as secondary parasites. This habit, since found to occur in other genera of Aphelininae, makes necessary special techniques in field colonization to effect establishment. After this discovery, it became clear why a number of earlier attempts to establish certain parasites of scale insects, mealybugs, and white flies had been unsuccessful.

The existence of biological and host-determined races, as mentioned in the discussion of the olive scale and others, has very much complicated the development to completion of many biological control projects. To date, the problems have involved mainly species of Eulophidae and Encyrtidae parasitic in scale insects, but the occurrence of such races is known in other groups and is probably much more frequent than is realized at present.

The possibility of developing new races or strains of parasite species, adaptable to specific climatic or other conditions, has intrigued biological control workers for many years, but only recently has this been attempted on an adequate basis. In studies on the development of cold-hardiness in *Dahlbominus fuscipennis* (Zetterstedt), Wilkes (111) found that the average temperature preferendum of both sexes is between 21.2 and 22.8° C., with two minor peaks at 15° C. and 9° C. In midsummer three nearly equal groups preferred temperatures of 25, 15, and 9° C., respectively. Continuous selection gave a marked increase in the percentage of individuals preferring the lower temperatures. An adaptive process in nature has produced the same results as those obtained by artificial selection in the laboratory. The breeding of strains with specific preferenda may have considerable practical value in the field colonization program. Very few entomophagous insects are adapted to the full climatic range of their hosts, many being limited to only a small portion of that range.

Preliminary experiments by Box (9) using the cane borer parasites *Metagonistylum minense* Townsend and *Paratheresia claripalpis* (van der Wulp) appear promising. Races of *Paratheresia* from Trinidad, Mexico, Venezuela and Peru were crossed, and the resulting hybrid from Venezuela-

Trinidad parents appeared to be the most vigorous and possibly best suited to Venezuelan conditions.

Evidence presented by Allen (2) indicates that a parasite species may become adapted to a host to which it initially was not attracted. Working with *Horogenes molestae* (Uchida), a parasite of the oriental fruit moth, he found that it could be induced to parasitize potato-tuberworm larvae only in the presence of larvae of its normal host. After several years of insectary rearing, however, it developed a high attraction for that host; the production in pure cultures of tuberworm larvae being 24 times that attained in the first tests. The question then arises as to whether this host-adapted strain retains its original attraction to its normal host when released in the field.

The sex ratio of laboratory stocks.—The problem of maintaining a favorable sex ratio in laboratory stocks is an important aspect in the economical mass production of many parasite species. On several projects the proportion of females in these stocks has declined progressively to the point where adequate numbers of females could not be produced, or the ratio of females became so low that even maintenance was impossible. By a process of selective breeding Wilkes (112) was able to demonstrate that this development can be reversed. A selective breeding program with *Dahlbominus fuscipennis* reduced the incidence of sterile males from 35 per cent to 2 per cent and at the same time increased the mean number of progeny per female from 38 to 68. These findings contributed substantially to the more economical production of the many millions of *Dahlbominus* utilized in the European spruce sawfly program. Simmonds (87) reports similar results in the rearing of the codling-moth parasite, *Mastrus* (*Aenoplex*) *carpocapsae* (Cushman).

Martin & Finney (68) improved the sex ratio of *Macrocentrus ancylivorus* by decreasing the light intensity in the mating room and by allowing a 24-hr. emergence period. They also found that the ratio of females increased with the degree of superparasitization. Flanders (42), working with the same parasite, found that multiple mating may result in prevention of fertilization of the female and reduced oviposition through crowding of spermatophores in the vagina.

The size of the host often has a very definite influence on the sex ratio of the parasite (14). This was strikingly demonstrated by Brunson (11) in the case of *Tiphia popilliavora* Rohwer, parasitic on the larvae of *Popillia japonica* Newman. Those developing on second-instar grubs were predominantly males, whereas on third-instar grubs the ratio was reversed. McGugan (65) found that the males of *Apechthis ontario* (Cresson) emerged mainly from male host pupae and females from female pupae, apparently the result of selective oviposition. Obviously, this factor of host size needs to be considered in developing techniques in some mass production programs.

Evaluation of parasite and predator effectiveness.—A great deal of difficulty has been experienced in evaluating the effectiveness of introduced or native natural enemies. Some progress has been made in this respect with those attacking scale insects and mealybugs in California. Smith & DeBach (92)

demonstrated that enclosure of infested branches in bags of fine-meshed cloth, to exclude the natural enemies, permitted a comparison of host development and increase with and without them. This study was later extended and modified by DeBach (22) in which trees were sprayed with DDT and talc, those treated with DDT showing a great increase of long-tailed mealybug while the trees receiving talc or no treatment showed a very marked decline in pest populations, due mainly to the activities of predators.

The cloth sleeve-test method mentioned above was later modified (24) to combine the features of both methods, the sleeve enclosing the branches being impregnated with technical DDT, and held in such a way as not to be in contact with the foliage. Check sleeves were untreated and open at both ends, permitting normal activity of natural enemies.

The question arose later as to the possible stimulating effect of repeated light applications of DDT on the pest insects themselves. It was shown (23) that such application had no appreciable effect upon populations of California red scale or yellow scale. The insecticidal check method offers a ready means of evaluating the effectiveness of natural enemies of pest species such as scale insects, mealybugs, and possibly whiteflies and mites.

The time factor in biological control.—The question of the length of time required for introduced parasites and predators to demonstrate their capacity for control of a pest in the field has long been of interest and concern to entomologists engaged in biological control activities. Because of the small numbers of the beneficial species released in relation to the large population of the host, it had been asserted frequently that a long interval is required before the full effectiveness of the introduced natural enemies is attained. This subject has been discussed by Clausen (16), who reviewed, insofar as detailed published data are available, all instances of what is generally accepted as full commercial control. These data indicated, without exception, that fully effective parasites and predators demonstrate very quickly their capacity for control of their hosts, and that this is achieved in the immediate area of release within three years, a period often representing only three host generations. This conclusion does not apply to partially effective parasites as their activities are strongly influenced by changing environmental influences. A species destined to be fully effective is always easily and quickly established and, conversely, the failure to become established easily and quickly is a definite indication that it will not be fully effective later. Various aspects of this problem are presented in criticisms of the above article by Thompson (100) and Sellers (84)

The Present Status of Biological Control

Any analysis of the present status of biological control of insect pests and a projection of developments into the future are of much interest and reveal a wide divergence of opinion, even among experts in the field. A provocative discussion of the subject is that by Taylor (99) who takes a definitely pessimistic viewpoint as to the possibility of worthwhile achievements in this field in the future, indicating that the cream has already been skimmed away and

the point of diminishing returns has long since been reached. Simmonds (88) presents a vigorous rebuttal to Taylor's thesis and cites many examples to illustrate the points at issue. Space limitations prevent an adequate review of these two articles, but a few points may be mentioned.

Taylor states

> . . . I know it [biological control] to be the best of all methods of controlling pests when it works, but that it seldom works and that there is little future for it in continental areas.

The successes in North America alone during the past 25 years are sufficient rebuttal to that statement. Systematic work in biological control of insect pests has hardly started in the great majority of continental countries, and there is every reason to expect results in those countries comparable to the successes achieved in North America and elsewhere. Accordingly, we may expect substantial progress in many areas in future years. Further,

> . . . the present tendency to organize the moving of parasites and predators about the world on an ever-increasing scale, despite decreasing results, is unsound and is, therefore, to be regretted.

A weighing of results of such recent work certainly refutes the assertion of decreasing returns.

The somewhat outmoded idea that insular conditions are in some way conducive to success in biological control is dealt with at some length by Taylor. That the most frequent successes in biological control have been attained on tropical islands is obvious from the record. These islands (Hawaii, Fiji, etc.) are characterized by a year-round equable climate, lacking cold winters and hot dry summers, and conditions are ideal for uninterrupted development of the natural enemies. Any departure from that ideal situation obviously reduces the chances of success. Hibernation, summer diapause, lack of alternate hosts, etc., enter into the picture, any one of which factors may cause a reduction in effectiveness or even prevent establishment of a natural enemy that under more favorable conditions would be fully capable of controlling its host. The greater degree of success in tropical island areas may be attributed, not to insularity as such, but to (*a*) optimum climatic conditions for development and increase of the natural enemies, and (*b*) the pest species occurring there are practically all of foreign origin and lack effective native control agents.

The need for intensive study of the ecological relationships of host and parasite is emphasized by both Taylor and Simmonds though qualified by a realization of the difficulties involved in supporting such researches on an adequate basis. At the present time, it is difficult to visualize the manner in which these detailed ecological studies can contribute substantially to the practices of applied biological control, insofar as the parasite introduction programs are concerned. For example, it is extremely doubtful that detailed studies of *Eretmocerus serius* Silvestri of Malaya, which so successfully controlled the citrus blackfly in the West Indies, would have revealed, in either or both countries, its complete ineffectiveness after establishment in

Mexico. Taylor's pronouncement to the contrary notwithstanding, biological control today is very largely on an empirical basis and will remain so for many years to come.

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BIOLOGY OF SCARABAEIDAE[1]

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The family Scarabaeidae is one of several families included in the superfamily Scarabaeoidea, a large distinct group of quite highly specialized beetles most easily recognized by their lamellate antennae. Various authors have proposed raising certain subfamilies to family rank such as the Geotrupidae [Paulian (117)], Hybosoridae [Gardner (52)], Pleocomidae [Paulian (118)], Acanthoceridae [Böving & Craighead (10)] and Trogidae [Leng (89)]. Crowson (26) recognizes six families in the Scarabaeoidea, the Lucanidae, Passalidae, Trogidae, Acanthoceridae, Geotrupidae and Scarabaeidae. Brues, Melander & Carpenter (16), however, divide the Scarabaeoidea into 22 families. They have even made families of such commonly accepted subfamilies as the Aphodiinae, Cetoniinae and Rutelinae and raised several tribes to family status.

Detailed studies of scarabaeid larvae, many of which were unknown to earlier workers, make it difficult to define as families such groups as the Geotrupinae. For this reason, such workers as van Emden (39) and the writer prefer to recognize only three families in the superorder, Lucanidae, Passalidae and Scarabaeidae. This is in accord with the classification followed by Blackwelder (8) in his checklist of coleopterous insects of Mexico, Central America, the West Indies, and South America.

The family Scarabaeidae according to Leng (89) includes 14 commonly recognized subfamilies, namely the Coprinae, Aegialiinae, Aphodiinae, Ochodaeinae, Hybosorinae, Geotrupinae, Pleocominae, Glaphyrinae, Acanthocerinae, Troginae, Melolonthinae, Rutelinae, Dynastinae, and Cetoniinae arranged as far as possible in phylogenetic sequence. My comments on the biology of the group will follow this order.

Published information on scarabaeid biology is exceedingly voluminous because of the world-wide distribution of the group and its diverse habits and because of the importance of many genera as crop pests. As in so many other fields, information on noneconomic forms is apt to be scanty and there is still much to be learned about such subfamilies as the Coprinae, Aphodiinae, and Troginae. Little is known about the biology of the Aegialiinae and Ochodaeinae. Habits of Coprinae, Geotrupinae, and Dynastinae are discussed by Arrow (3) who gives an interesting account of the habits of horned beetles but many of his conclusions are based largely on inferences from their morphology. Howden (75) presents an excellent summary covering the biology and taxonomy of Geotrupinae from the world standpoint.

[1] The survey of the literature pertaining to this review was completed in May, 1957.

Food Habits

Leng (89) has suggested that food is the chief environmental factor affecting beetles and that this factor is correlated with profound structural modifications. Certain it is that food is one of the most important considerations in the biology of scarabaeids both for larva and adult, and the structure of both is adapted for particular feeding functions.

Food of adults.—In Table I may be found some general conclusions about the food preferences of adult scarabaeids. It will be noted that the subfamilies fall into two main groups, one group including such subfamilies as the Coprinae, Aphodiinae, Geotrupinae, and Troginae which are either saprophagous or fungus feeders and a second including the subfamilies Melolonthinae, Rutelinae, Dynastinae, and Cetoniinae which are strictly phytophagous. This diversity of habit has been long recognized and the family has often been divided into the so-called lamellicorn scavengers and the lamellicorn leaf chafers [Comstock (23)]. This also corresponds in general to the division into the groups Laparosticti and Pleurosticti based on the position of the spiracles [Blatchley (9); Hayes (66)].

TABLE I

Food Habits of Scarabaeids

A = Adults L = Larvae

SUBFAMILY	SAPROPHAGOUS										PHYTOPHAGOUS			
	Carrion		Dung		Humus		Decaying Veg. Matter		Duff	Litter	Wood		Fungi	Seed Plants	
Coprinae	A	L	A	L			A						A		
Aphodiinae	A	L	A	L		L	A	L					A		L
Geotrupinae	A		A	L		L		L	L	L			A		
Acanthocerinae											L				
Pleocominae															L
Glaphyrinae								L							L
Troginae	A	L													
Melolonthinae						L								A	L
Rutelinae						L					L			A	L
Dynastinae				L		L		L	L	L	L			A	L
Cetoniinae				L		L					L			A	

According to Leng (89), feeding upon decaying substances is a primitive food habit for Coleoptera, while the habit of feeding on living plant tissue is found in more specialized forms. For this reason Leng and many others have considered the lamellicorn scavengers the more primitive of the groups.

Adults of the Coprinae and Aphodiinae are known to feed on carrion, dung, decaying vegetable matter, and fungi (56, 76, 99, 141). Pessoa & Lane (124) have mentioned some of the food habits of Coprinae found in Brazil. Pereira (121) describes the unusual case of the coprine beetle *Zonocopris gibbicollis* (Harold), which feeds on the slime of snails. The various species of *Aphodius* feed commonly in dung or decaying organic matter. In England,

adults of *Aphodius fimetarius* Linnaeus and *Aphodius subterraneus* Linnaeus, which are common in horse manure, also injure mushrooms by devouring portions of the caps (2).

There is now a considerable body of literature on the food habits of Geotrupinae (1, 73, 75, 87, 116, 143, 152, 155, 167, 174). Adults of some species of *Geotrupes* feed only on dung while others feed either on dung or on fungi [Howden (75)]. The same writer observed adults of *Bolboceras* (formerly *Odontaeus*) *darlingtoni* (Wallis) feeding on fungi. According to Fabre (44), adults of *Bolbolasmus* (formerly *Bolboceras*) *gallicus* (Mulsant) also feed on fungi.

Adults belonging to the Pleocominae (genus *Pleocoma*) never feed. The same is also true for adults of the Glaphyrinae (genus *Lichnanthe*) [Franklin (49)].

Although the lamellicorn leaf chafers may be placed in one general group on the basis of their feeding on living tissue, there is in reality a great diversity in their food habits. Adults of Melolonthinae and Rutelinae devour plant tissues, especially leaves, flowers or young fruits. In contrast, adults of Dynastinae usually attack stems or roots of plants in their search for liquid nourishment, often feeding underground. Adults of the Cetoniinae are also largely liquid feeders, but feed above ground, preferring nectar or sap or the juices of ripening fruits and vegetables. Some species feed on pollen. There are species in each of the subfamilies Melolonthinae, Rutelinae, and Dynastinae which do not feed at all in the adult stage.

Adults of many species of Melolonthinae are voracious feeders on the leaves of various plants, particularly those of shrubs and trees. Thus beetles of several species of *Melolontha* often defoliate trees in many parts of Europe (86, 130). Many species of *Phyllophaga* frequently defoliate trees in the United States and Canada (19, 100, 136, 145). Adults of both genera are crepuscular or nocturnal.

In Malaya, adults of *Apogonia cribricollis* Burmeister and *Apogonia expeditionis* Ritsema attack the leaves of cacao [Lever (91)]. In the Sudan, adults of *Schizonycha* feed on the leaves of *Dolichos* [Pollard (128)]. Johnson (80), in the United States, found adults of *Polyphylla decemlineata* feeding on the needles of ponderosa pine. According to Dumbleton (33) adults of the grass grub *Castelytra* (*Odontria*) *zealandica* (White), occurring in New Zealand, prefer foliage of rosaceous plants, sometimes causing severe defoliation of fruit and ornamental trees. The same species has also been responsible for severe damage by defoliating cruciferous seedlings.

Other melolonthine adults feed either on blossoms or young fruits. In the United States, adults of *Macrodactylus subspinosus* (Fabricius) often injure young fruit of grapes, apples, and peaches (144). Adults of *Hoplia callipyge* Leconte devour the blossoms, young leaves, and fruit of many different plants along the Sierra foothills of California [Essig (43)].

Adults of *Amphimallon majalis* Razoumowsky do not feed, according to Gyrisco *et al.* (60). This also holds true for adults of *Cochliotis melolonthoides* (Gerstaecker) in Tanganyika [Jepson (78)].

Adults of ruteline leaf chafers feed commonly on leaves, fruits, and blossoms. In the United States, the introduced Japanese beetle, *Popillia japonica* Newman, has been found feeding on over 275 species of plants including tree and bush fruits, shade trees, corn, soybeans, and many ornamentals [Hawley & Metzger (62)]. In feeding on foliage small portions of the leaf surface are consumed resulting in a skeletonized appearance.

Many species of *Anomala* have similar habits [Hayes & McColloch (67); Lupo (98)] but a few species feed little or not at all. Laughlin (88) reports that adults of *Anomala horticola* (Linnaeus) do not need to feed for mating and egg laying to occur. Friend (51) found that the adults of *Anomala orientalis* Waterhouse feed very little and concluded that they fed only to obtain moisture. According to Bradford (13), adults of *Anomala vetula* Weidemann, occurring in Africa, have not been observed to feed.

In Malaya, adults of *Chaetadoretus cribratus* (White) and *Adoretus compressus* (Weber) feed on the leaves of cacao [Lever (91)]. In southern Chile, the adults of *Hylamorpha elegans* (Burmeister) feed on the leaves of *Nothofagus obliqua* and *Prunus avium* [Duran (35)].

The main food of dynastine beetles is the juice of living plants obtained most often from the underground stems, shoots, or tap roots. Thus adults of *Strategus quadrifoveatus* (Palisot de Beauvois) attack the base of coconut sprouts undergound and may even feed on the juices of older coconut palms [Plank (126)]. Adults of several species of *Euetheola* (*Dyscinetus*) are pests of rice, maize, and sugar cane in various parts of the world, working underground where they gnaw into the heart of the plants or cut the young shoots [Baerg (4); Kern (81); Phillips & Fox (125)]. In the United States adults of *Ligyrus gibbosus* DeGeer feed on the underground parts of carrots, sunflowers, celery, sugar beets, and potatoes [Hayes (63)].

Adults of *Heteronychus licas* Klug, in Mozambique, damage young maize, rice, and sugar cane [del Valley y March (162)]. In Kenya, Le Pelley & Goddard (119) found that adults of *Heteronychus consimilis* Kolbe feed extensively on the young shoots of wheat, just below the surface. In Australia, adults of the introduced species *Heteronychus sanctae-helenae* feed on a wide variety of field, vegetable, and fruit crops and on ornamentals [Wallace (166)]. Depending on the crop, damage is caused by underground feeding on the tap roots, on stem bases, in tubers (potatoes), on cuttings (sugar cane, grape vines), or on suckers (bananas). Fruits resting on the ground are also injured.

In northern Venezuela, Box (11) and Guagliumi (59) report adults of *Podischnus agenor* (Olivier) damage sugar cane by boring into the stalks. The same species damages young bamboo plantations in Central America and is an important pest in sugar cane in Guatemala and Colombia [Box (12)].

Adults of *Oryctes rhinoceros* (Linnaeus), widely distributed in southern Asia and the East Indies, have different habits from the above species in that they work in the tops of coconut and other palms [Gressitt (58); Nirula,

Antony, & Menon (111)]. This results in damage to the growing point and destruction of leaf tissue. According to Gressitt (58) the beetle does not ingest solid plant material, but sucks the juices from the macerated tissue.

Adults of some species do not feed. This is true of *Cyclocephala immaculata* Olivier and *C. borealis* Arrow, commonly found in eastern United States [Ritcher (138); Johnson (79)].

Adults of many species of Cetoniinae feed on plant juices, either sap or juices of ripening or overripe fruit. Other species are common on flowers where they feed on pollen or nectar. Most species are diurnal in habit.

Adults of *Cotinis nitida* (Linnaeus) occurring in eastern United States, feed on ripening fruits, on tomatoes, corn in the milk stage, and the sap of oak and other trees (140). Adults of *Cotinis texana* Casey have similar habits and also feed on pollens of sorghum, corn, cotton and other plants [Nichol (110)]. Adults of several species of *Euphoria* have similar habits and in addition frequent flowers where they secure nectar or pollen (140). Hoffman (70) in his monograph on *Trichiotinus* states that beetles of this genus feed on pollen.

According to Korschefsky (84) adults of *Cetonia aurata* Linnaeus damage blossoms and fruits in Germany. He reports that adults of *Potosia aeriginosa* Drury are found on flowers and at tree sap and adults of *Potosia cuprea* Fabricius damage blossoms and occasionally bore into ripe fruits. Adults of *Valgus canaliculatus* (Fabricius), common in eastern United States, feed on the nectar of flowers [Ritcher (140)].

Food of Larvae.—The food habits of scarabaeid larvae do not lend themselves to easy division into a few distinct groups (Table I). There are some plant feeders among the larvae of the lamellicorn scavengers and dung feeders among the larvae of the lamellicorn leaf chafers. It is true, however, that the majority of the dung and carrion feeding forms belong to the lamellicorn scavengers (Laparosticti) and the majority of the root feeding forms belong to the lamellicorn leaf chafers (Pleurosticti). Unlike adult scarabaeids, no scarabaeid larvae are definitely known to feed on fungi, although this habit has been suspected by various writers.

The food of coprine larvae is provided by the adults and is discussed in a later section on nidification. Dung is the larval food of most species; others feed on carrion [Pessoa & Lane (124)] or feathers [Howden & Ritcher (76)]. Some genera such as *Deltochilum* utilize all three kinds.

Aphodiine larvae are predominately dung feeders but some kinds feed on organic matter in the soil and a few species prefer the roots of living plants. Downes (32) and Ritcher & Morrison (148) have described injury to turf by larvae of *Aphodius pardalis* LeConte, in North America. In Minnesota, Hoffman (69) observed larvae of *Ataenius* injuring grass roots. In Australia and Tasmania *Aphodius howetti* Hope and *Aphodius pseudotasmaniae* Given cause extensive damage in pastures [Erlich (42); Martyn (102)].

Nothing is known about larvae of the Ochodaeinae. According to Gardner (52) larvae of Hybosorinae are found in soil or in dung.

Larvae of most species of Geotrupinae feed on such materials as dung, humus, duff, or litter, all provisioned for them by the adults [Howden (75)]. Larvae of the European *Lethrus aptrus* Laxman feed on leaves, buds and shoots of grapes and other plants, which have been cut by the adults and packed into underground cells [Schreiner (152)]. Some species, such as *Geotrupes blackburni* Fabricius, use either dung or leaf duff for the larval food [Howden (75)]. Larvae of *Geotrupes ulkei* Blanchard feed on decomposing leaves [Loding (96)].

The interesting subfamily Pleocominae is found only in western North America, being especially common in Oregon and California. Larvae of several species of *Pleocoma* feed on tree roots [Ritcher & Olney (149); Ellertson (38)], but I have found larvae of one species in California, feeding on grass roots (142).

Published accounts of the feeding habits of glaphyrine larvae have been few. According to Franklin (49) working in Massachusetts, larvae of *Lichnanthe vulpina* (Hentz) were found damaging the roots of cranberries as early as 1911 and had become a considerable pest by 1917. My observations in Oregon show that larvae of *Lichnanthe rathvoni* LeConte feed on decaying leaves and other organic matter in sandy areas along streams. Although locally abundant, none have ever been found injuring crops.

Information about acanthocerine larvae is also scanty. Lugger (97) mentions rearing *Cloeotus* and mentions that the larval food is decaying material beneath the bark of dead trees. Hesse (68), in discussing African Acanthocerinae, states that according to Ohaus the food of the larvae is rotten wood.

Larvae of Troginae are usually found feeding in soil beneath carcasses of dead animals. A few species, as will be mentioned later, feed on grasshopper eggs [van Emden (40)].

The lamellicorn leaf chafers include many species whose larvae are of economic importance because they prefer to feed on the roots of living plants. These belong principally to the Melolonthinae and in part to the Rutelinae and Dynastinae. At the same time, there are also many species whose larvae feed on humus, duff, decaying organic matter, or decaying wood. This is the case with most larvae of the Cetoniinae, with many dynastine larvae and with some ruteline larvae.

De Fluiter (47), working in Java, divided white grubs into 3 categories, according to their feeding habits: (*a*) grubs feeding only on dead organic matter (Cetoniinae); (*b*) grubs which normally feed on dead organic matter but will attack living roots in its absence (certain Rutelinae and Dynastinae); (*c*) grubs feeding by preference on living roots of crop plants (Melolonthinae). In other parts of the world, numerous members of the Rutelinae, such as the Japanese beetle (*Popillia japonica* Newman) and the Chinese rose beetle (*Adoretus sinicus* Burmeister), also belong in the third group.

In many parts of the world, larvae of Melolonthinae cause extensive damage to the roots of grasses, legumes, small fruit plants, shrubs and trees. Larvae of greatest economic importance belong mainly to the tribes Melo-

lonthini or Sericini. First-stage larvae feed, in part, on organic matter in the soil; second and third instars feed largely on roots or underground stems.

Throughout Europe larvae of the genus *Melolontha* are of major importance, attacking grasses, vegetable crops, and the roots of young trees (14 18, 77, 130). *Amphimallon* larvae are destructive to the roots of field and forage crops, lawns and nursery stock both in Europe and in the northeastern United States [Gyrisco *et al.* (60)]. In North America, from Mexico to Canada, larvae of many species of *Phyllophaga* cause widespread damage to roots of pasture grasses, corn, Irish potatoes, and tree seedlings (9, 19, 135). In Chile, larvae of *Phytolaema*, *Sericoides* and *Shizochelus* cause extensive damage to cereal and forage crops [Duran (35)].

The most injurious species of melolonthine larvae in New Zealand belong to the genus *Costelytra* (*Odontria*) [Given & Hoy (55)], but *Calonota* larvae are also important [Cumber & Cowie (27)]. In India, *Leucopholis* larvae injure the roots of coconut palms and also attack cassava, sweet potatoes, yams and *Colocasia* [Nirula, Antony & Menon (111)]. In Java, larvae of *Lepidiota*, *Holotrichia* and *Psilopholis* feed on the roots of rubber trees [de Fluiter (47)]. In Africa, in Sudan, larvae of *Schizonycha* feed on peanuts and the roots of sorghum [Pollard (128)].

In Tanganyika, Jepson (78) reports that larvae of *Cochliotes melolonthoides* (Gerstaecker) cause extensive damage to the roots of sugar cane. Other melolonthine larvae of economic importance are species of *Cnemarachis* in the West Indies [Wolcott (172)] and the genus *Clemora* (*Phytalus*) in Mauritius and Barbados [Box (12)].

Of the Rutelinae, larvae of species belonging to the Anomalini usually feed on roots of living plants. A few species of the Rutelini feed on living roots, but many others belonging to such genera as *Pelidnota* and *Parastasia* feed on decaying wood (139). In the Philippines, a few feed on decaying vegetable matter [Viado (163)].

Larvae of various species of *Popillia*, *Anomala* (including *Phyllopertha*), all belonging to the Anomalini, are of economic importance. Larvae of *Phyllopertha horticola* (Linnaeus) injure grass roots in England (104, 105, 129). Larvae of *Anomala vetula* Wiedemann injure roots of turf in South Africa [Bradford (13)]; in Japan larvae of *Anomala albopilosa* Hope injure roots of pine wind breaks [Nitto & Tachibana (113)]. In Virginia, larvae of *Strigoderma arboricola* (Fabricius) damage peanuts [Grayson (57)]. Mitchell (106) reports that in Rhodesia, grubs of *Anomala* and *Adoretus* feed primarily on rotting vegetation in the soil but occasionally damage tobacco transplants.

In the United States, larvae of the introduced Japanese beetle, *Popillia japonica* Newman, cause extensive damage to turf grasses [Pepper & Gesell (120); Schread (151)]. Smith & Hadley (156) made a careful analysis of the contents of the fore-gut of larvae collected in grass sod and found that 64.3 percent of the material consumed was from roots of living plants. The balance consisted of decayed plant tissue (19.6 per cent) and mineral matter (16.1 per cent).

Of all the subfamilies, larvae of the Dynastinae exhibit the most diverse food habits. Preferred foods for larvae of the various species include dung, humus, decaying vegetable matter, litter, duff, decaying wood, and the roots of living plants. There is even provisioning for the larvae by adults of certain species (*Strategus*).

According to de Fluiter (47) dynastine larvae occurring in Java rubber plantations normally feed on dead organic matter but will also attack living roots. Jepson (78) found in Tanganyika that larvae of *Heteronychus tenuistriatus* Fairmaire usually feed on decaying roots and detritus but, when numerous, damage live roots of sugar cane. Larvae of *Heteronychus licas* Klug, in Mozambique, feed on organic matter in the soil, in wet low-lying areas beside rivers [del Valley y March (162)]. Larvae of *H. consimilis* Kolbe, however, in Kenya, damage the roots of wheat (119). In the United States, larvae of the rice beetle, *Dyscinetus trachypygus* (Burmeister) feed in compost or in soil near pig pens [Phillips & Fox (125)].

In the United States, larvae of *Cyclocephala immaculata* Olivier feed both on decaying organic matter and on roots of grasses and grain (138). Martelli (101) states that larvae of *Pentodon punctatus* Villers feed on grapevine cuttings. According to Plaut (127) *Pentodon* larvae damage roots of young apple trees and seedlings in Israel.

Food habits of *Oryctes* larvae in various parts of the world also vary greatly (25). In India, larvae of *O. rhinoceros* feed in cattle dung [Nirula, Antony & Menon (112)], but Gressitt (58) found that larvae of this same species feed on dead wood, compost, or dung in the Palau Islands. In Germany, Korschefsky (84) reports that older larvae of *Oryctes nasicornis* Linnaeus are found in compost heaps, manure, tanning beds, old piles of street sweepings, and sawdust piles.

Larvae of Cetoniinae almost never feed on the roots of living plants. Instead, they feed commonly on decaying vegetable matter in the soil, on dung, or in dead wood. Larvae of such genera as *Trichiotinus* and *Osmoderma* feed largely on wood [Hoffman (72); Ritcher (140)]. *Valgus* larvae feed on the walls of termite burrows in logs or standing dead trees (140).

Some cetoniine larvae cause plant injury but this results from disturbance of the soil and roots rather than from feeding. In this way, larvae of the green June beetle, *Cotinis nitida* Linnaeus, have recently caused extensive injury to ladino clover pastures and lawns in the southeastern United States [Davich *et al.* (29)].

Nidification

Nest building or the provision made by adults for their progeny has been studied in some detail by a number of European workers [Fabre (45); Schreiner (151); Lengerken (90)], but has been paid little attention in this country. Strangely enough, while looking after the future needs of the larva is usually the rule among beetles of the subfamilies Coprinae and Geotrupi-

nae, both subfamilies of so-called lamellicorn scavengers, this habit also occurs among certain species of *Strategus* belonging to the subfamily Dynastinae, a subfamily of the lamellicorn leaf chafers. Although the Coprinae are popularly known as tumble bugs, actually only a few genera, such as *Canthon* and *Deltochilum*, roll balls (141). *Copris* and *Phanaeus* form balls, but this is done in an underground chamber [Lindquist (92, 93)]. Most other genera pack tubular burrows with food materials for their larvae.

The ball of *Canthon* and *Copris* is usually composed of dung; that of *Phanaeus* has a center of dung and an outer covering of soil. The ball of *Deltochilum*, which the adult rolls, has a core of fur or feathers. This is later coated with mud and the whole is wrapped in pieces of dead leaves (76). Unlike *Canthon*, *Deltochilum* does not bury its ball but places it within a shallow cup-like depression in the soil, beneath fallen leaves. This is quite similar to the habits of *Nesosisyphus* in the island of Mauritius described by Vinson (164).

Adults of *Geotrupes blackburni* (Fabricius) provision a shallow burrow with an elongate, more or less horizontal wad of dung or duff in which they lay a single egg [Howden (75)]. According to the same writer, adults of *Bolboceras* (*Odontaeus*) and related genera provision their burrows with humus obtained from the top-most layer of soil.

Species of *Strategus* differ in the provision they make for their larvae. Larvae of *Strategus quadrifoveatus* (Beauvois), found in Puerto Rico, feed in wood and the adults make no provision for their larvae other than laying their eggs in small cells having walls composed of minute pieces of wood mixed with soil [Plank (126)]. Adults of *Strategus mormon* Burmeister, however, provision burrows with horse dung and therein deposit their eggs [Knaus (83)].

In North Carolina *Strategus antaeus* (Fabricius) has been found to provision its burrow with surface litter such as pine needles. The entrance to the burrow is marked by a pushup of sand and the burrow often has the shape of an inverted Y. Adults are active in August; small larvae may be found feeding in the mass of litter in September.

Number of Molts

It has generally been believed that all scarabaeids, without exception, have three larval instars. Thus, van Emden (39) states "the larvae of the Lamellicornia moult thrice, the third ecdysis releasing the pupa." Floyd Ellertson and the writer, in studying the biology of several species of *Pleocoma* in Oregon, have found that larvae of this peculiar genus may molt from 7 to 11 times with one molt occurring each year.

Pupation Habits

The mature scarabaeid larva constructs a cell in which to pupate. A prepupal stage precedes actual pupation. Some dung feeding larvae such as cer-

tain species of *Aphodius* pupate in cells within the old dung mass, but most dung feeding species pupate in the soil. Larvae of *Geotrupes blackburni* make a cell in the soil within the old dung or duff mass stored there by the female (75). Wood feeding forms such as *Osmoderma* prepare a pupal case made of wood fragments or of humus-like material accumulated in tree cavities [Hoffman (72)]. Soil inhabiting forms such as *Phyllophaga* make an elongate cell in the earth (136).

In most subfamilies the last larval skin is pushed to the rear of the pupal cell, but in the subfamily Rutelinae the pupa is cradled in the inflated larva skin which first splits longitudinally along the middorsal line (13, 15, 51). Most dynastids have similar habits, however, in a few genera such as *Oryctes* [Gressitt (58)] and *Strategus*, the pupa pushes the larval skin to the rear.

The time of year when pupation occurs varies within most subfamilies and often varies within a single genus (Table II). For example, I have found that in the genus *Anomala*, *Anomala nigropicta* Casey and *Anomala binotata* Gyllenhal pupate in the fall, overwinter as adults, and appear in flight early the next spring. In the same locality *Anomala innuba* (Fabricius) overwinters as a full grown larva, pupates in the spring and does not appear in flight until early June (137). Similarly, most species of *Serica* common to the eastern United States pupate in the fall, overwinter in the soil as adults, and fly in the early spring. In California, in contrast, I have found that most species of *Serica* overwinter as full grown larvae and pupate in the late winter and early spring (144).

A summary of information on pupation gleaned mostly from the literature or based on personal observations is given in Table II. It will be noted that the average length of the pupal stage, under field conditions, is a minimum of 14 days and may be much longer. Exact information on this point is difficult to obtain and is lacking for several species. In laboratory studies Vogel & Ilic (165) have shown that the length of the pupal period for *Melolontha melolontha* Linnaeus varies with the temperature, being 3 to 4 months at 12° C. and 4 to 5 weeks at 20 to 25°C.

Pupation habits of Phyllophaga.—A detailed study of the pupation habits of several species of *Phyllophaga*, made several years ago by the writer, serves to emphasize the fact that species, even though closely related taxonomically, are distinct entities biologically (136). This basic fact is often ignored by those engaged in economic work.

Like species of *Serica* and *Anomala* some species of *Phyllophaga* pupate in the summer while others pupate in the spring (Table II). Those pupating in the summer (July or August) remain within their pupal cells for part or all of the winter, depending again upon the species, and then emerge in the spring to feed on foliage. Species such as *Phyllophaga ephilida* (Say) overwinter as full grown larvae, pupate in June and appear in flight, as adults, in July.

The depth of pupation is also characteristic for each species, seemingly

regardless of latitude (136). *Phyllophaga hirticula* (Knoch) was found to pupate at an average depth of 12.3 to 15.6 in. in Kentucky, while *Phyllophaga inversa* (Horn), another summer-pupating form, averaged from 4.5 to 6.9 inches in depth in the same localities. *Phyllophaga ephilida* (Say), a spring-pupating form, averaged only 3.3 in. in pupation depth.

Length of Life Cycle

Scarabaeids' life cycles vary with the climate, being longest in more temperate regions. The shortest life cycles are to be found in tropical areas with no climatic seasons [Gressitt (58)]. Life cycles may be comparatively long in some regions having a dry, hot season since larvae may aestivate for several months until the rainy season begins [Moutia (107)].

The life cycles of many scarabaeids have been worked out in detail but those of such subfamilies as Aphodiinae, Troginae, and Acanthocerinae are little known. According to Madle (99), large species of *Aphodius* have one generation a year, while smaller species have two. In general, in temperate regions, the Coprinae [Cooper (24); Lindquist (93)] and most Geotrupinae [Howden (73, 75)] have life cycles of one year. In Oregon we have evidence that the life cycle of *Pleocoma* spp. (Pleocominae) is very long, perhaps requiring eight or more years. In the Melolonthinae, Rutelinae, Dynastinae and Cetoniinae the life cycles may be one, two, or three years or in the case of the Melolonthinae, even four or five years in northern latitudes.

In the Melolonthinae, most species of the tribe Melolonthini have rather long life cycles, especially in temperate regions. In the United States the many species of *Phyllophaga* have a two- or three-year life cycle [Hayes (65, 66); Reinhard (133, 134, 135); Ritcher (136)]. Some species having a three-year cycle in the northern states may have only a two-year cycle in states south of the Ohio River (136), while some species having a two-year cycle in the northern states have only a one-year cycle in Texas [Reinhard (131, 132)].

In Europe, *Melolontha hippocastani* Linnaeus requires from three to five years to complete its life cycle according to Korschefsky (84) and Schwerdtfeger (154) while *Melolontha melolontha* Linnaeus requires from three to four years depending upon latitude [Regnier (130)]. Work by Thiem (159) with *Melolontha* spp. indicates that differences in the length of life cycle of a given species depend on the rate of development of the first and second instars. In Germany, the life cycle of *Polyphylla fulla* Linnaeus takes three or four years [Korschefsky (84)].

Species belonging to the Melolonthine tribes Sericini and Macrodactylini usually have a one-year life cycle, but some species in more temperate climates have a two-year cycle. In the United States it appears that *Macrodactylus* and various species of *Serica* require one year for the complete life cycle. Schread (151) states that *Autoserica castanea* Arrow also has a one-year life cycle. According to Murayama (109), *Serica orientalis* Motschulsky

TABLE II

PUPATION HABITS OF SOIL INHABITING SCARABAEIDAE

Species	Subfamily	Time of Year	Av. Length of Stage	Depth Range	Depth Av.	Country	Reference
Geotrupes blackburnii	Geotrupinae	Sept.	17.5 days	3–6.5″	4″	United States	(75)
Bolboceras darlingtoni	Geotrupinae	June	24 days	8–12″	10″	United States	(75)
Pleocoma dubitalis	Pleocominae	July–Aug.	—	5–9.5″	7″	United States	(146)
Pleocoma crinita	Pleocominae	Aug.–Sept.	—	9–21″	12.5″	United States	
Lichnanthe rathvoni	Glaphyrinae	May–July	—	3–10″	6.4″	United States	
Phyllophaga ephilida	Melolonthinae	June	19.5 days	2–6″	3.3″	United States	(136)
Phyllophaga hirticula	Melolonthinae	July	27.2 days	7.5–23″	14.6″	United States	(136)
Polyphylla decemlineata	Melolonthinae	June	—	5–7.5″	6.5″	United States	
Melolontha hippocastani	Melolonthinae	August	38–40 days	—	—	Switzerland	(170)
M. hippocastani & *M. melolontha*	Melolonthinae	—	—	14–16″	—	Prussia	(153)
M. melolontha	Melolonthinae	Mar.–Aug.	5–6 wk.	—	12–14″	England	(45)
Amphimallon majalis	Melolonthinae	May–June	15 days	2–10″	—	United States	(60)
Costelytra zealandica	Melolonthinae	Oct.	6 wk.	—	12″	New Zealand	(33)
Cochliotis melolonthoides	Melolonthinae	Feb.–Sept.	14 wk.	12″–3′	—	Tanganyika	(78)
Anomala vetula	Rutelinae	Nov.–Jan.	30 days	9–12″	—	South Africa	(13)
Anomala orientalis	Rutelinae	June–July	14 days	3–12″	—	United States	(51)
Phyllopertha horticola	Rutelinae	April–May	4 wk.	.8–3.8″	2″	England	(105)
Popillia japonica	Rutelinae	May–June	14 days	—	—	United States	(155)
Cyclocephala immaculata	Dynastinae	May–June	16 days	3–6.5″	3.6″	United States	(136)
Euetheola rugiceps	Dynastinae	Aug.–Sept.	14 days	—	—	United States	(125)
Cotinis texana	Cetoniinae	May–June	—	2–5″	—	United States	(110)
Cotinis nitida	Cetoniinae	May–June	16–18 days	3–8″	—	United States	(31)

has a one-year life cycle in Manchuria and Korea. In New Zealand, *Costelytra* (*Odontria*) *zealandica* (White) also has a one-year life cycle [Dumbleton (33)].

In the Rutelinae, few detailed studies have been made of the length of cycle for species belonging to the Rutelini. Hoffman (71), working in Kansas, U.S.A., reports a two-year life cycle for *Pelidnota punctata* (Linnaeus). My work in Kentucky indicated that this species and *Parastasia brevipes* (LeConte) each have a two-year life cycle (139). Hayes (65) reared 21 individuals of *Cotalpa lanigera* (Linnaeus) and found that this species has either a two- or three-year life cycle.

Because of the great economic importance of the Anomalini, many workers have made detailed studies of their life cycles (13, 15, 51, 57, 64, 104, 105). *Popillia japonica* Newman, *Anomala orientalis* Waterhouse, *Anomala kansana* Hayes and McColloch, *Anomola innuba* (Fabricius), *Anomala nigropicta* Casey and *Strigoderma arboricola* (Fabricius) all have one-year life cycles in the United States. *Phyllopertha horticola* (Linnaeus) has a one-year life cycle in Sweden [Brammanis (14)] and England [Raw (129); Milne (105)]. Friend (51) states that a few larvae of *Anomala orientalis* Waterhouse have a two-year life cycle in Connecticut. The same is true for *Anomala albopilosa* Hope in Japan [Nitto & Tachibana (113)].

Species of Anomalini having a two-year life cycle include *Anisoplia segetum* Herbst in Germany [Korschefsky (84)] and *Anomala vetula* Wiedemann in South Africa [Bradford (13)].

Little information is available about the life cycles of species belonging to other tribes of the Rutelinae. *Hylamorpha elegans* (Burmeister), belonging to the tribe Anoplognathini, is said to have a one-year life cycle in southern Chile [Duran (35)]. Mitchell (106) states that in Rhodesia *Adoretus* sp. (belonging to the Adoretini) also has a one-year life cycle.

In the United States, a number of species belonging to the Dynastinae such as *Cyclocephala immaculata* Olivier, *Euetheola rugiceps* (LeConte), *Ligyrus gibbosus* DeGeer and *Xyloryctes satyrus* (*Fabricius*) have one-year life cycles (63, 65, 125, 136, 138). My work indicates that *Dynastes tityus* (Linnaeus) has a two-year life cycle. Gressitt (58) studied *Oryctes rhinoceros* (Linnaeus) in the Palau Islands where there are no discernible climatic seasons. He found that, given favorable conditions, more than three generations may develop in one year.

Detailed rearing work by Plank (126) in Puerto Rico shows that the average length of the complete life cycle of *Strategus quadrifoveatus* (Palisot de Beauvois), from egg to first oviposition is 595 days. My studies in North Carolina, indicate that *Strategus antaeus* (Fabricius) has a two-year life cycle.

In northern Venezuela, *Podischnus agenor* (Olivier) apparently has a one-year life cycle, according to Guagliumi (59). In France, *Pentodon punctatus* Villers has a one- or two-year life cycle [Martelli (101)]. *Pentodon idiota* Herbst is said to have a three-year life cycle [Tchouvakhine (158)].

Such genera of the subfamily Cetoniinae as *Cotinis*, *Euphoria*, *Trichio-*

tinis and *Valgus*, all of which occur in the United States, have one-year life cycles (31, 65, 70, 110, 140). *Osmoderma erimicola* has a two- or three-year life cycle depending on latitude [Hoffman (72)]. *Gnorimus octopunctatus* Fabricius, which occurs in Germany, has either a two- or three-year life cycle according to Korschefsky (84).

Mating Habits

Mating between males and females of the same species is the usual thing among scarabaeids and, in fact, the sclerotized, accessory genital processes of both male and female are so constructed that cross-mating between most species is physically impossible. However, in the case of closely related species some evidence has been found that cross-mating does occur and that hybrids may be produced.

Some years ago, in examining many thousand *Phyllophaga* adults at the Madison, Wisconsin, Federal White Grub Laboratory, we ran across a few individuals, perhaps one in 5000, which appeared to represent a cross between *Phyllophaga hirticula* (Knoch) and *Phyllophaga rugosa* (Melsheimer). When one considers that the male *Phyllophaga* must find his mate at night, from among thousands of individuals often including some six or more other species, all feeding on the same tree, the wonder is that more such hybrids are not produced.

Failure to find morphological differences between larvae of *Cyclocephala immaculata* Olivier and *Cyclocephala borealis* Arrow, two closely related, common dynastine species, once led me to investigate the possibilities of interbreeding. In the laboratory, males of *C. borealis* mated freely with females of *C. immaculata*. Eggs were laid and appeared to develop normally but the fully formed larvae were never able to emerge. In comparable matings between beetles of the same species, development proceeded normally.

Mating sites.—Choice of mating sites varies with the subfamily and from genus to genus within some subfamilies. Beetles of the genus *Geotrupes* (Geotrupinae) and of *Pleocoma* (Pleocominae) mate in burrows in the soil [Howden (75); Smith & Potts (157)]. *Geotrupes splendidus* (Fabricius) mates in the fall, but eggs are not laid until the following spring (75). Similar habits for *Pleocoma* have been found in California and Oregon [Ritcher & Beer (146)].

Among the Melolonthinae, many species of *Serica*, *Diplotaxis*, and *Phyllophaga* mate at night while the female continues feeding on foliage. Other melolonthine beetles such as *Hoplia* and *Macrodactylus* mate on flowers in the daytime. Among the Dynastinae, mating of some genera such as *Ligyrus* occurs in the soil. Cumpston (28) found that adults of *Heteronychus sanctaehelenae* Blanchard and *Metenastes vulgivagus* Olliff copulate beneath the surface of the ground. Other genera such as *Cyclocephala* mate on the surface of the soil with many males fighting for possession of a single female.

Of the Cetoniinae, genera such as *Trichiotinus* and *Trigonopeltastes* mate on flowers. In *Valgus*, mating occurs within termite galleries in stumps or fallen trees.

Interrelationships with Other Insects

Scarabaeids exhibit a number of interesting relationships with other insects, in addition to those with insect parasites and predators which will be discussed in a later section. Some scarabaeids are actually predaceous on other insects while many species of the Cetoniinae are myrmecophilous or termitophilous.

Of the Coprinae, *Canthon deplanatus* var. *fastuosus* Harris is predaceous in Brazil upon the queen ants of *Atta* spp. using the dead body of the female as a component of the ball in which its larva later develops (from correspondence with E. Navajas). *Canthon conformis* Harris and *Canthidium* sp. seem to be occasional predators of the same ants. According to Pereira (122) *Haroldius philippenensis* Pereira was found associated with ants of the genus *Diacamma* by P. J. Darlington of Harvard, on Luzon Island. *Haroldius heimi* Wassman has been found in nests of *Pheidole latinoda*.

Aphodius porcus Horn is a predator in the egg cavity of *Geotrupes stercorarius* Linnaeus [Chapman (20)]. After destroying the egg of the *Geotrupes*, this aphodian lays its eggs in the dung mass which the geotrupid had provided for its own larva. What appears to be a similar case, involving *Aphodius lividus* (Olivier) as a "parasite" of *Onthophagus medorensis* Brown, is reported by Howden (74).

Among the Troginae, larvae of two species of *Trox*, *Trox procerus* Harold and *Trox suberosus* Fabricius, are known to prey on grasshopper eggs and are of considerable economic importance [van Emden (40)].

Beetles of several genera of the subfamily Acanthocerinae are termitophilous [Hesse (68)]. *Philharmostes* is associated with termites in Madagascar and Costa Rica and two species of *Acanthocerus* are associated with termites in Brazil. Both larvae and adults appear to feed on rotten wood [Ohaus (114)].

Numerous genera of the Cetoniinae are known to be associated with ants or termites throughout the world [Wheeler (169)]. Myrmicophilous genera include *Cremastocheilus* in the United States (169); *Plagiochilus* and *Myremecochilus* in South Africa [Wasmann (168)]; *Placodidus*, *Tricholoplus*, *Scaptobius* and *Lissogenius* in South Africa [Peringuey (123)]; and *Potosia cuprea* Fabricius in Germany [Korschefsky (84)]. Termitophilous genera are *Coenochilus* in South Africa [Wheeler (169)], and *Valgus* in many parts of the world.

Wheeler concludes that beetles of the genus *Cremastocheilus* are degenerate symphiles which may have once been of use to the ants but are now persecuted intruders (synechthrans). The larvae of *Cremastocheilus* and of certain *Euphoria* apparently feed within the vegetable debris of the ant colony. Both genera are usually associated with ants of the genus *Formica*.

Lee Townsend of the University of Kentucky and the writer have made numerous observations on the biology of *Valgus canaliculatus* (Fabricius) and *Valgus seticollis* (Beauvois), both common in the nests of the termite *Reticulitermes flavipes* (Kollar). A third species, *Valgus californicus* Horn, is

found in California associated with termites of the genus *Zootermopsis nevadensis* (Hagen) [Linsley & Michener (94)].

All stages of *Valgus* may be found in decaying wood associated with termite colonies. The larvae apparently feed on the walls of the old termite galleries. Pupation of *Valgus canaliculatus* occurs in July and early August within small oval cells constructed of wood fragments or soil (140). Colonies of *V. canaliculatus* contain males and females in almost equal numbers; colonies of *V. seticollis* usually contain a great majority of females.

Natural Enemies

Pleurostict scarabaeids are attacked by many parasites and predators. Among the parasites are mites, Diptera, Hymenoptera, bacteria, fungi, protozoa, and nematodes. Common predators are various mammals, fish, birds, amphibians and certain Coleoptera, Hymenoptera, and Diptera. Of the four life stages, larvae and adults have the greatest number and variety of natural enemies.

Insect parasites.—Insect parasites attacking melolonthine, ruteline, and dynastine larvae include many species of Tiphiidae and Scoliidae, and numerous species of Tachinidae [Clausen (20)]. Less common insect parasites of these scarabaeid larvae are one species belonging to the Pelecinidae [Forbes (48)], one ichneumonid [Davis (30)], and several species of bombyliids (20). Parasites of adult scarabaeids belong mainly to the family Tachinidae but include several species of pyrgotids and a few species of sarcophagids.

No insects are known to be parasitic on scarabaeid eggs but several dipterous parasites of pupae have been recorded. Handlirsch (61) describes a nemestrinid parasite on pupae of *Amphimallon solstitialis* Linnaeus in Europe. Asilid and bombyliid larvae have been found parasitizing *Phyllophaga* pupae in the United States (30, 136, 147).

Tiphiid and scoliid wasps are fossorial, seeking out grubs both in the soil and in decaying wood [D'Emmerez de Charmoy (41); Clausen (21)]. Eggs are deposited singly and the parasite larvae feed externally on the paralyzed scarabaeid grubs. Host identity can often be determined, at least to genus, by examination of the head capsule, usually found attached to the parasite cocoon.

Some of the factors governing host selection are host size, host habitat, and synchronization with the host's biology [Dumbleton (33) and Given (54)]. These principles have been utilized in attempted biological control of such important pests as the Japanese beetle *Popillia japonica* (Newman), *Clemora smithi* (Arrow), *Costelytra zealandica* (White), and *Oryctes* spp. (22, 41, 54, 108). Members of the genus *Tiphia* tend to be limited to a host genus, or to closely related genera [Gardner & Parker (53); Clausen, King & Teranishi (22)]. In Australia, Burrell (17) found several genera of Thynninae exhibiting similar preferences for grubs of a certain genus.

Some Tiphiids and scoliids are remarkably specific as to host [Lloyd (95)

and Guagliumi (59)]. Several species of thynnid parasites occurring in Chile are each restricted to a single host species [Lloyd (95)]. According to King & Holloway (82), in the Orient, strains of *Tiphia popilliavora* Rohwer which are indistinguishable morphologically differ in their distribution and seasonal appearance and select different host species of *Popillia*.

Bacteria, fungi and *rickettsiae*.—Larvae of soil-inhabiting scarabaeids are often attacked by bacterial disease, and most workers with this group of insects have observed epizootics at one time or another. Davis in his review of the natural enemies of *Phyllophaga* states that up to 1919 only one bacterial disease (that caused by *Micrococcus nigrofaciens* Northrup) of white grubs was known to occur in the United States although at least two diseases of related species were known in Europe (30).

Dutky, in 1940, described two new sporeforming bacteria, *Bacillus popilliae* Dutky (Type A) and *Bacillus lentimorbis* Dutky (Type B), causing milky diseases in the Japanese beetle (36). These have since been used widely in the United States in the biological control of the beetle [Beard (6)]. According to Dumbleton a native bacillus, distinct from *B. popilliae*, causes a milky disease in larvae of *Odontria zealandica* White, in New Zealand (34). Recently, Beard has described two milky-disease bacteria from Australian scarabaeids, *Bacillus lentimorbis* var. *Australis* Beard affecting *Sericesthis pruinosa* (Dalman) and *Bacillus euloomarahae* Beard affecting the introduced *Heteromychus sanctae-helenae* Blanch (7).

The fungus *Metarrhizium anisopliae* (Metchnikoff) is an important factor in white-grub control in several continents. In one area of Algeria, Moutia found 90 per cent of the *Geotrogus* larvae attacked (107). In the United States, Nichol (110) reports this fungus parasitic on larvae of *Cotinis texana* Casey, and Philips and Fox (125) mention all stages of the dynastid *Euetheola rugiceps* (LeConte) as susceptible to infection. The same fungus is known to infect the rhinoceros beetle (*Oryctes*). In Germany, Schaerffenberg found that *Beauveria densa* (Link) could cause up to 90 per cent mortality of *Melolontha* larvae (150). The spectacular *Cordyceps* fungus, mentioned by Davis, has long been known as a sporadic parasite of scarabaeid larvae (30). Apparently several species of *Cordyceps* are involved.

Coxiella popilliae Dutky & Gooden, the cause of a rickettsial disease of *Popillia japonica* and *Phyllophaga* larvae, was described in 1952 (37). According to Krieg (85) "lorsch" disease of *Melolontha* larvae in Europe is caused by the same or a closely related rickettsia, which he has described as *Rickettsia melolontha* Krieg.

Insect predators.—Major insect predators of scarabaeids are certain Asilidae, Tabanidae, Carabidae, Elateridae, Histeridae, and Formicidae. Less common insect predators belong to the Ithonidae (Neuroptera), Coenomyiidae, Mydidae and Passalidae. Larvae of scarabaeids are most subject to attack.

Asilid larvae are important predators of soil-inhabiting scarabaeids (21).

Davis lists 13 species as probable predators of *Phyllophaga* larvae (30). In Australia, Miller records larvae of two native asilids as predators of *Odontria* larvae (103). Lupo mentions *Asilis* sp. as predaceous on *Anomala* larvae (98).

Several species of tabanid larvae appear to be predaceous on *Phyllophaga* and *Cyclocephala* larvae (30). In two instances I have observed *Coenomyia* (Coenomyiidae) larvae attacking scarabaeid larvae, once in North Carolina attacking a *Trox* larva and once in Oregon attacking a *Dichelonyx* larva.

Balduf (5) reviews the literature on Carabidae, Elateridae and Histeridae all important predators of scarabaeids. Carabid adults prey on both adults and larvae, and sometimes on eggs. Gyrisco *et al.* (60) found carabid predators of *Amphimallon majalis* Razoumowsky extremely abundant. Grubs in an experimental plot were largely destroyed by *Harpalus pennsylvanicus* DeGeer and *Harpalus erraticus* Say was an important egg predator. According to Gressitt (58) carabids prey on both adults and larvae of the coconut rhinoceros beetle, *Oryctes rhinoceros* (Linnaeus), in the Palau Islands.

Elaterid larvae of a number of genera prey on scarabaeid larvae in soil, decaying wood and in dung. *Alaus* and *Ctenicera* are predaceous on *Oryctes* larvae [Freiderichs (50)], as are also *Pyrophorus* larvae [O'Connor (115)]. Xambeau (173) mentions *Corymbites cupreus* Fabricius consuming larvae and pupae of *Aphodius*. Wolcott (171) mentions larvae of *Pyrophorus luminorus* Illiger as important predators of May beetle grubs in Puerto Rico.

Importance of histerids as predators of *Oryctes* larvae in and their use in biological control of *Oryctes* is discussed by Gressitt (58) and O'Connor (113). Both adults and larvae of some species feed on first instar *Oryctes*. Lupo records larvae of *Hister major* Linnaeus attacking larvae of *Anomala ansonia* var. *neopolitana* Reitter (98). Balduf (5) reviews records of histerids predaceous on larvae of *Aphodius*, *Teuchestes*, *Oxythhyrea* and *Cetonia* in Europe.

Several writers mention the importance of ants as predators of eggs and young larvae of scarabaeids (98). In 1926 Tillyard worked out the life history of a neuropteron, *Ithone fusca* Newman, which is a predator of melolonthine larvae in Australia (160, 161). Jepson (78) mentions finding larvae of a passalid, *Didimus sansibaricus* Harris which were feeding on *Cochliotis* larvae, in Tanganyika.

Vertebrate predators.—In some insular areas amphibians are important predators of scarabaeids. The Surinam toad, *Bufo marinus* Linnaeus, introduced into Puerto Rico about 1920 by Box (12) soon became so numerous that white grubs entirely disappeared from cane fields [Wolcott (171)]. A ground lizard, *Ameiva exsul* Cope, destroys eggs and larvae of May beetles in the same island. In Illinois, frogs, toads, and salamanders are mentioned as predators of *Phyllophaga* (30).

Many writers record instances in which birds are predaceous on both larvae and adults of soil-inhabiting scarabaeids. Moutia (107) states that in

France thousands of insectivorous crows, *Trypanocorax frugileus* Linnaeus, were observed feeding on larvae of *Melolontha melolontha* Linnaeus. In Morroco, he reports that the cattle egret, white stork, and blackbirds feed on *Amphimallon*, *Rhizotrogus* and *Anoxia* larvae. Other birds mentioned as predaceous on scarabaeid larvae include domestic fowl, meadow larks, owls, starlings, robins, song sparrows, grackles, pheasants, cat birds, woodpeckers, gulls and thrushes (30, 31, 51, 60, 125).

Among important mammalian predators are moles, hogs, shrews, coyotes, ground-squirrels, badgers, field mice, racoons, foxes, and skunks (30). In the United States the skunk is probably the most important predator. In the eastern half of the United States it feeds voraciously on *Phyllophaga* and *Amphimallon* larvae (30, 60). In Oregon, the skunk *Mephitis occidentalis* Baird is the main predator of adult *Pleocoma*. I have seen orchards in the Hood River Valley where as many as 25 adults have been dug from their burrows, beneath a single apple tree.

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INSECT ERADICATION PROGRAMS

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Elimination of a biological entity from a sizeable area is a challenging approach to an age-old problem. Undesirable insects, disease organisms, nematodes, weeds, rodents, even birds, frequently create economic problems when they are permitted entry into new areas. "From time immemorial," said Parrott (1), "inroads of injurious insects on agriculture have been regarded as inevitable handicaps for which there was little or no amelioration." This is no longer true.

We find no references in literature prior to the late 19th century indicating that anyone seriously considered the possibility of eradicating an insect once established in a new land. The theory of eradication thus can be considered as relatively new.

The term "eradicate" means to destroy, remove utterly, complete destruction, or removal in general; thus "exterminate" is a synonym. To the professional entomologist, "eradication" means extermination or elimination of an insect population, and the term is generally applied with reference to an incipient infestation of an insect new to an area or not widely distributed.

We now have a background of experience that permits us to draw some conclusions. Some 30 years of experience in suppressing incipient infestations of pests introduced into the United States provide data on which to measure success or failure as the case may be.

Growth in Acceptance of Eradication Principle

Early settlers in North America recorded relatively few pestiferous insects; most of these more or less localized. They wrote about mosquitoes, biting gnats, certain forest insects, grasshoppers, and nose bots from deer. North America was amazingly free of the insect pests that are of such economic importance today—insects that now levy a tax on the agricultural economy estimated to be at least four billion dollars a year.

Early migrants to this country brought in, on their bodies, such parasites as lice, mites, and fleas. In their bedding and sea chests came bed bugs, clothes moths, and carpet bettles. Associated with their livestock and poultry were lice, fleas, and mites. The ships upon which our ancestors crossed the ocean brought the horn fly, stable fly, numerous species of bottle flies, and many other insects now common to all continents. Such importation of insect pests accelerated with shipments of raw commodities necessary to sustain a rapidly growing population with its developing industrial interests.

It was not until about 1890 that entomologists began to question the free flow of agricultural commodities from foreign countries without some safeguard against insects associated with them. They began to appraise the number of serious insect problems traceable to such commerce. It has been estimated that in the 58 years prior to 1912 at least 92 species of economically

important insects had been introduced into the United States. Included were such well-known insects as the horn fly, asparagus beetle, gypsy moth, San Jose scale, European red mite, greenbug, Argentine ant, boll weevil, and the alfalfa weevil, to name only a few.

It finally became obvious to the entomologists of that day, but not so clear to commercial interests, that measures could and should be taken short of embargo which would exclude many foreign insects from this country. The Plant Pest Act passed by Congress in 1905 was the first positive step in this direction on a national scale. This was followed by the Plant Quarantine Act of 1912. This Act authorized the Secretary of Agriculture to enforce such regulations as he considered necessary to protect the agricultural economy of this country from insects and plant-disease organisms associated with importations from foreign countries.

It is interesting to note that since 1912 only some 30 insects of foreign origin are on record as having become established in the United States. This marked reduction in the rate of importations (about one-third that of the previous 58 year period) has occurred despite a tremendous increase in the volume of imports, in international travel, and the speed with which travel is performed.

Exclusion by quarantine thus appears to be effective. Also, relatively speaking, exclusion appears to be an inexpensive means of protecting this country from foreign insects of economic importance. There are some 2000 of these subject to interception by plant quarantine inspectors at ports of entry into the United States.

The action taken in the late 1880's by Massachusetts legislators with regard to an appropriation for the suppression or eradication of the gypsy moth was the first organized attempt to eradicate an insect in the United States. The gypsy moth, *Porthetria dispar* (Linnaeus), was deliberately brought into Massachusetts in 1869 by a person who sought to revolutionize the silk industry. The insect escaped from his laboratory to nearby woodlands in the vicinity of Medford, Massachusetts, where it multiplied undisturbed for the next 20 years. "By 1889," according to Hinds (2),

> their numbers had become enormous. They stripped the trees of Medford; over-ran streets and homes. In 1890, the Massachusetts Legislature made the first appropriation for the control or eradication of this pest. The fight was so well waged that the pest was held within an area of less than 400 square miles for the next ten years and moths became so scarce they were rarely seen. Extermination seemed almost accomplished.
>
> Then—State appropriations were withheld, the work stopped for 5 years, and the moths multiplied so rapidly during this time that an area of fully 4,000 square miles became infested. By 1905, extermination was considered impossible.

Smith (3) expressed the opinion of many entomologists in 1885 when he said

> There is nothing, . . . , to prevent the spread of this insect over the entire United States, except the limitations imposed by nature itself. Just what they are remains to be seen.

A few years later, in 1898, Osborn (4) declared,

> The heroic effort made by Massachusetts to exterminate the gypsy moth is one of the best and most effective arguments for a system of exclusion, the cost of which would be slight compared with the loss entailed by an imported pest.

However, Marlatt (5) was not convinced that eradication was either possible or feasible. He said in 1899,

> An effort which seems to me to be often of questionable utility is that directed toward extermination. I have already alluded to the fact that not a single notable case of extermination of an insect at all well established, has been effected by the agency of man; nor do I believe that such results will ever be accomplished.

There was, however, a strong conviction on the part of some entomologists that something more positive could and should be done. The American Association of Economic Entomologists, in 1907, passed the following resolution and sent it to each United States Congressman:

> Congress should authorize the Secretary of Agriculture to proceed to exterminate or control imported insects or plant diseases or any insect previously native to a restricted locality, but which may become migratory and threaten the whole country, whenever, in his judgment, such action is practicable, and that an appropriation be made for this purpose as a reserve fund for emergency use against any such pest which may arise.

This resolution represented aggressive thinking—but it lacked the unanimous support of the Association. Those who fostered it relied heavily on things to come; they had little to point to in the way of accomplishment.

It was extremely difficult during these early years for entomologists to overcome hopeful thinking that natural enemies of insects offered the most practical approach to all entomological problems. The theory of biological control led many to rationalize against the more difficult, controversial, and costly cultural and chemical eradication or control procedures.

Recent Developments in Insect Quarantine

Nearly a quarter of a million lots of unauthorized plant material were intercepted during 1956 at United States ports. From these were taken many of the world's most destructive agricultural pests. For example. the Mediterranean fruit fly was intercepted 162 times, citrus canker 139 times, black spot of citrus 128, golden nematode 26, pink bollworm 164, olive fruit fly 17, and the durra stem borer 6. The value of the port-of-entry inspection can hardly be questioned.

The job of inspecting the tremendous volume of imports since World War II, including baggage of incoming travelers, has severely taxed quarantine facilities. Thousands of travelers arrive daily from points throughout the world. Air transportation, in particular, has increased the threat of world-wide spread of destructive insects. A few figures will serve to illustrate how the problem of quarantine has grown in the past ten years.

"Foreign plant quarantines," according to Annand speaking before the

TABLE I

INCREASE OF QUARANTINE INSPECTION IN THE UNITED STATES IN THE PAST TEN YEARS

Articles Inspected	No. inspected Fiscal Year 1948	No. inspected Fiscal Year 1957
Aircraft	58,046	110,944
Vessels	43,496	49,560
Railway cars	73,893	106,355
Vehicles	6,787,099	18,453,115
Pieces of baggage	4,456,307	15,623,378
Pieces of air cargo	322,582	1,292,748
Mail and express parcels	2,826,725	8,789,574
Import shipments	64,107	79,595
Export shipments	9,177	47,592
Shipments from Hawaii and Puerto Rico inspected	4,943	6,987
Interceptions of unauthorized plant material	137,341	290,854

American Association of Economic Entomologists at Richmond, Va., Dec. 1946 (unpublished),

undoubtedly have been helpful to prevent establishment of the thousands of destructive pests which have not yet gained entrance to this country. No doubt such quarantines will continue to be available in the future. But these, and domestic quarantines to restrict their spread, do not present the perfect barrier to plant pest introduction and dissemination visualized by many.

At best quarantines are a compromise between the perfect protection desired, and the necessities of a country whose citizens must have commercial intercourse with their neighbors, whether foreign or domestic. Perfect protection from artificial movement of pests would mean cessation of all trade and travel between quarantined and unquarantined areas.

It must be granted that no system of inspection can be infallible. Numerous destructive foreign pests have penetrated our first line of defense—a defense that steadily improves as time passes. But what to do about an established infestation of an insect new to this country has been a matter of controversy over the years.

SOME SUCCESSFUL ERADICATION EFFORTS

Mediterranean fruit fly.—When the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), invaded Florida in 1929, the program that followed proved conclusively that the eradication of at least some introduced insects was feasible. As described by Hinds (2),

The discovery in April 1929 that the Mediterranean fruit fly had become established in the heart of the Florida citrus area, spread alarm to the entire southern

portion of the United States. Florida State authorities took prompt, extensive, and effective action—Congress made available appropriations required. Never before was such an extensive and thorough control put into effect so quickly. A large, trained force of inspectors quickly outlined the infested area. Destruction of infested fruit, spraying of trees with poisoned bait for adult flies, and other control measures went forward with amazing speed and efficiency.

Within three months after discovery the extensive infestation, which involved about 75 per cent of the citrus area of the State, was practically stamped out. Only three very small infestations were found thereafter. The whole undertaking was a complete success.

The accomplishment of this eradication effort . . . constitutes one of the most outstanding achievements of applied entomology anywhere in the world.

It would be difficult to place a dollar value on benefits accruing to the citrus and soft-fruit industries of this country, or, for that matter, to the consumer, from the successful eradication of the Mediterranean fruit fly in Florida. For 25 years following that often-called "costly" effort, the United States was the only major citrus and soft-fruit producing country in the world to remain free of the Mediterranean fruit fly and the oriental fruit fly *Dacus dorsalis* (Hendel).

Date Palm Scale.—Another operation worthy of note pertains to the eradication of the date palm scale, *Parlatoria blanchardii* (Targioni). This pest came into the United States, according to Marlatt (5),

when the United States Department of Agriculture introduced some half hundred small date palms from Egypt and Algeria . . . (in 1890) . . . . These proved to be thickly infested with scale insects and were kept at the Department under surveillance and treatment for six months, being subjected some dozen times to various methods of treatment, and were ultimately distributed and planted. In spite, however, of the strenuous effort made to destroy the scale insects in question, and the apparent absolute freedom of the plants from the presence of the scale when sent out, it needed merely a year or two for the scales to develop as badly as ever. In fact, on account of the overlapping and clasping of the basal part of the leaves of the palm, it proved to be absolutely impossible to reach and exterminate the scale secreted there by any means whatsoever short of killing the plant.

Some years later, however, the date scale was eradicated with tremendous savings to both producer and consumer. While Marlatt was right in saying "no method was known to deal with the pest during the time of importation," methods later were developed that were effective and the desired objective was accomplished. Eradication of the date scale, while less spectacular than that of the Mediterranean fruit fly in 1929 is no less convincing of what can be done if there is the will to do—and the tools to do with. This program proved that eradication, at least to some degree, is a frame of mind.

Citrus Canker.—The eradication of citrus canker (caused by the bacterium *Xanthomonas citri*), although not an insect, presented many of the same kind of problems commonly encountered in dealing with an incipient infestation of an insect. The benefits accruing from the successful eradication

of this disease from the United States are equally impressive—and just as difficult to measure in a monetary way.

Such successful efforts at eradication, combined with more recent advances in entomological research, together with an ever-increasing vigilance at our ports of entry, have brought about a gradual change in the thinking of many entomologists as to the possibilities that exist for protecting agriculture from foreign pests.

Advances in insect eradication methodology are not easily evaluated. Through experience, however, we have learned that isolated infestations of a number of recently introduced pests can be eliminated with facilities available today.

A comparison of the current Mediterranean fruit fly eradication program with that of 1929 serves to illustrate both advances in technical knowledge and in public thinking. The objective, eradication, was the same in both instances. But the approach was drastically different.

"The 1929 campaign," according to Sherman (6),

> involved an almost frenzied "scorched-earth" policy to rid the area of all host material, cultivated or wild, ornamental or commercial. Considerable public resentment was engendered because of the compulsory destruction of crops without compensation and drastic interference with commercial fruit and vegetable production and marketing.

The urge for quick eradication was just as imperative in 1956 but methods of attack were radically different. The 1956 contention was that the fly should have easy access to hosts to discourage distant flight. Quarantine regulations recognized that established spray schedules applied to vegetable crops were so effective that they eliminated all sprayed vegetables in sparsely infested areas as potential sources of spread. Soon after an infestation was discovered by means of the greatly superior lures used, an airplane swooped in with a lethal poison-bait spray that attracted and killed nearly 100 per cent of the adult flies even when coverage was incomplete. Repeated at frequent intervals, there was a sudden near eradication of fly population.

It is not possible to discuss early attempts to exclude or eradicate an introduced pest without making further reference to the gypsy moth since in this case there has been an uninterrupted program of quarantine and control since 1907. At least three generations of entomologists have questioned the value of organized suppressive work since this insect first drew the attention of the Massachusetts Legislature in 1890. Only persistent efforts and a deep-seated belief in the principles of preventive entomology have kept the gypsy moth confined to the area it presently occupies, when an environment probably much more to its liking awaits it in the Southern Appalachian and Ozark regions.

Methods of Dealing with Foreign Insect Introductions

We are now able to draw comparisons, after some 75 years of experience in the handling of six major insect problems in the United States: Japanese beetle versus European corn borer, Mexican bean beetle versus white-fringed beetle, and boll weevil versus pink bollworm.

Japanese beetle—European corn borer comparison.—The Japanese beetle problem and the European corn borer problem were contemporary. Since they were handled so differently, it is of interest to compare the long-time results of such handling.

The Japanese beetle, *Popillia japonica* Newman, was found in New Jersey in 1916. The extent of the infestation at that time indicated that the insect probably had been in the United States some nine or ten years—or perhaps even longer. A Federal quarantine was established in 1919. Natural spread has not been stopped; however, as of this date, only about $6\frac{1}{2}$ per cent of the area of the United States is infested (see Fig. 1). As a part of the containment effort, numerous outlying infestations have been eradicated. Through regulatory measures, long-distance spread largely has been prevented. Artificial controls have been greatly improved over the years. A number of parasites have been introduced and successfully colonized for the biological control of the pest. Uninfested portions of the country can now be protected indefinitely from the Japanese beetle without burdensome cost if we make intelligent and aggressive use of what we know.

The European corn borer, *Pyrausta nubilalis* (Hübner) entered the United States, apparently in a shipment of Hungarian broom corn, about 1907, in the vicinity of Boston, Massachusetts. When discovered in 1916, it had spread over some 400 square miles. By 1921, when quarantines were established, it was known to infest limited areas in Ohio, New York, Massachusetts, Connecticut, and Ontario, Canada.

There was widespread disagreement at this early date as to the value of suppressive work. Against all entomological advice, Congress appropriated 10 million dollars in 1928 to eradicate the European corn borer. Equipment was devised to cut corn stubble short and deep-plow remaining trash. Such equipment was used on thousands of infested acres. Reduction of infestation was estimated to be 98 per cent or more in many treated fields. But the potential destructiveness of the pest was underestimated. In 1932 the corn borer quarantine was revoked. Research was continued, but no further effort was made to suppress or contain the infestation. The corn borer (see Fig. 2) now infests all major corn-growing areas north of central Oklahoma, Arkansas, Mississippi, Alabama, and Georgia; and east of the Rockies. This insect caused more loss to corn belt farmers in 1949 than all regulatory and control costs against it would have equalled in 100 years even had costs of such work trebeled over the years.

It was extremely difficult in the early thirties for entomologists to know what course to pursue in dealing with an introduced pest. "One of the most treacherous trails that the entomologist travels," said Houser (7),

> is that of a newly introduced insect, because it is difficult to judge exactly what policy to follow. He may expect serious damage and thus launch a vigorous program of research to meet the situation, only to find, after he has expended money and effort, that he has misjudged the seriousness of the problem and that his resources might well have been expended along some other line. Again, it is an equally serious mistake

to under-emphasize a situation in its incipient stages and thus allow something really serious in nature to get beyond control.

From the standpoint of our economy, the holding operation against the Japanese beetle is thus shown to have been very much worthwhile.

White-fringed beetle—Mexican bean beetle comparison.—Another interesting comparison can be made in the handling of the white-fringed beetle and the Mexican bean beetle.

The white-fringed beetle, *Graphognathus leucoloma* (Boheman), a native of South America, was found in northwest Florida in 1936. This insect is a general feeder; the adults attack more than 170 kinds of plants, its grubs feed on the roots of some 385 different plant species. Full federal-state regulatory procedures have been taken against the insect since it was first reported. Under continuous regulatory and quarantine attention, it has been confined to relatively small areas aggregating some 600,000 acres in eight southeastern states (see Fig. 3). No infestation has been found following treatment for three years or more on about 25 per cent of this area. New insecticides and new methods of applying them bring ever closer to reality the hope that the white-fringed beetle can be eradicated.

No regulatory or control measures were ever initiated against the Mexican bean beetle, *Epilachna varivestis* Mulsant, until it reached California. There, an infestation involving 3462 acres was stamped out over a period of $9\frac{1}{2}$ years at a cost of about $980,000. Today, California is free of this pest.

The Mexican bean beetle, thought to be a native of Mexico, was found in Alabama in 1920. It usually feeds on beans, but it will attack soybeans and cowpeas, and sometimes, in heavy infestations, alfalfa, clovers, vetch, and certain grasses. Isely (8) said, " . . . within its range [this insect] is the most destructive pest of the bean plant." The Mexican bean beetle was allowed to spread at will. Even though its feeding is limited to a narrow range of food plants, by 1935, only 15 years later, the Mexican bean beetle infested most of the area east of the Mississippi River; by 1955 (see Fig. 4), portions of Louisiana, Arkansas, Missouri, Iowa, and Wisconsin, as well.

Boll weevil—Pink bollworm comparison.—A third and equally interesting comparison can be made between the handling of the boll weevil, *Anthonomus grandis* Boheman, and the pink bollworm, *Pectinophora gossypiella* (Saunders).

When the boll weevil reached Texas in 1892 and began its uninterrupted march eastward across the Cotton Belt, it caught entomologists divided in their opinions as to what could or should be done. Research was started immediately. By 1903, when most of eastern Texas was infested, most entomologists were in agreement that cotton farmers would have to live with the pest. Demonstration plots were established in east Texas to show farmers how to grow cotton in competition with the weevil. The weevil crossed the Mississippi River in 1912, and the whole of the Cotton Belt was infested just 20 years later (see Fig. 5). By 1952, 60 years after it entered the United States, this insect had caused losses in cotton production aggregating some 5 billion dollars.

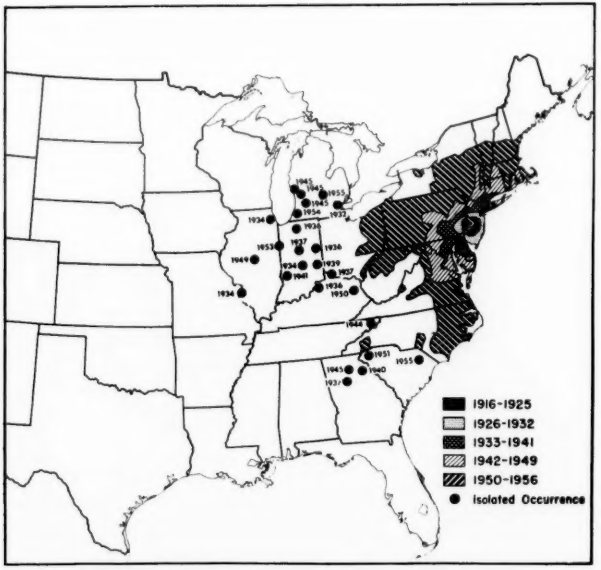

FIG. 1. Spread of the Japanese beetle, 1916–1956.

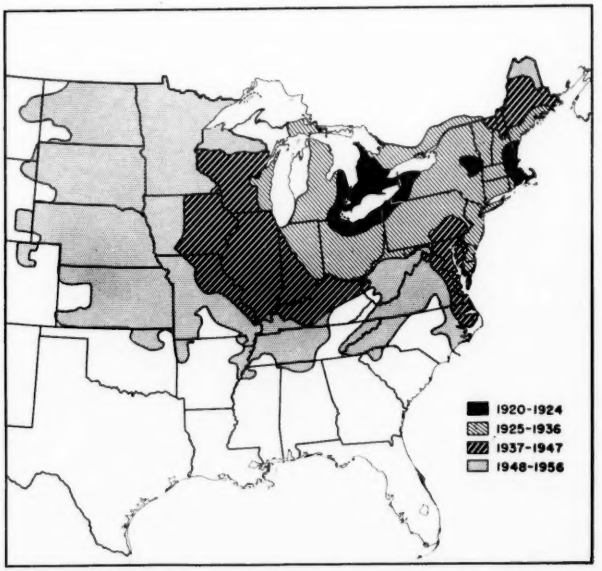

FIG. 2. Spread of the European corn borer, 1920–1956.

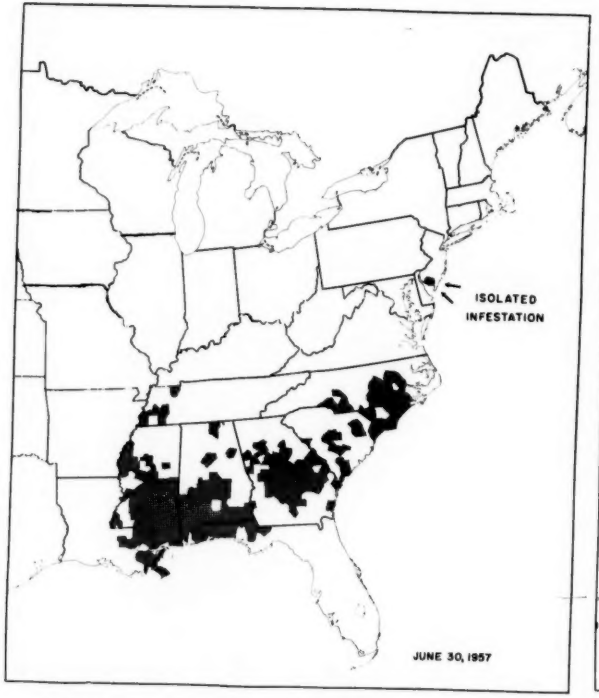

FIG. 3. Known distribution of the white-fringed beetle.

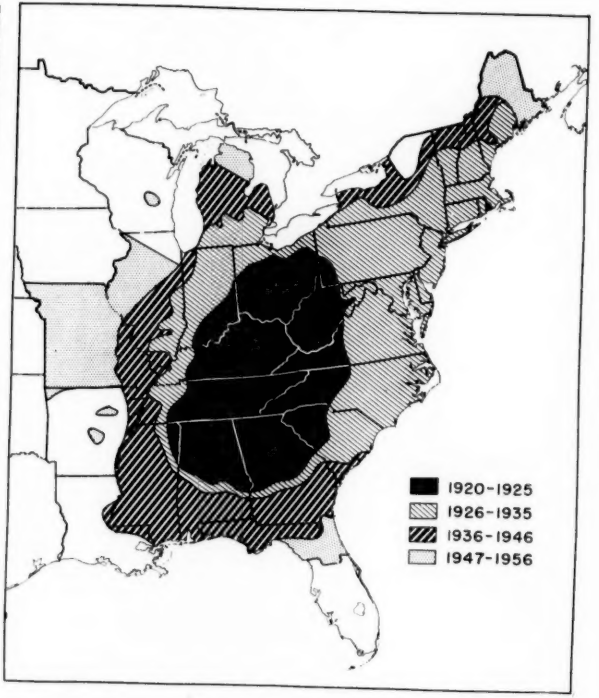

FIG. 4. Spread of the Mexican bean beetle, 1920–1956.

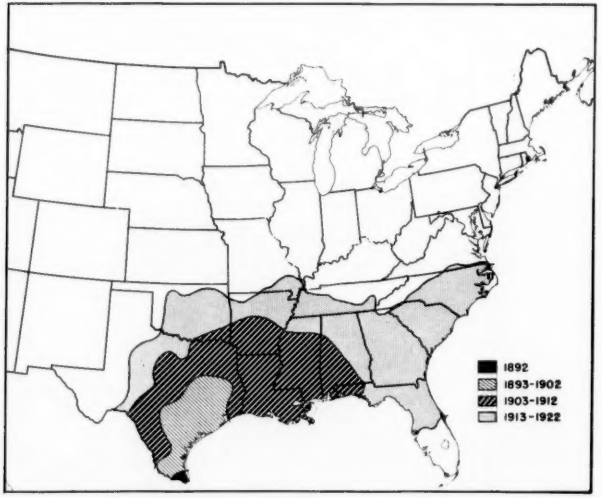

FIG. 5. Spread of the boll weevil, 1892–1922.

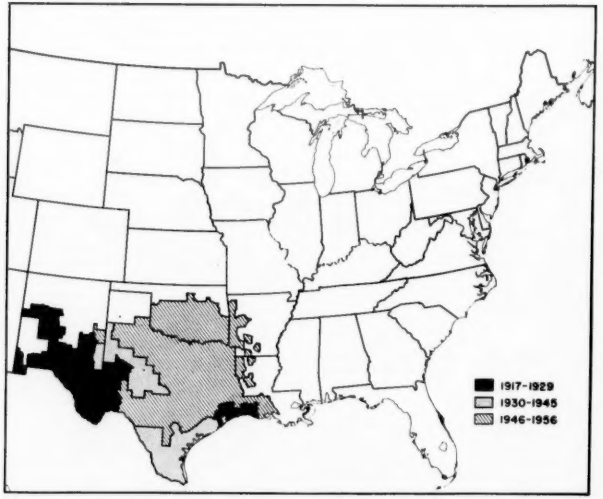

FIG. 6. Spread of the pink bollworm, 1917–1956.

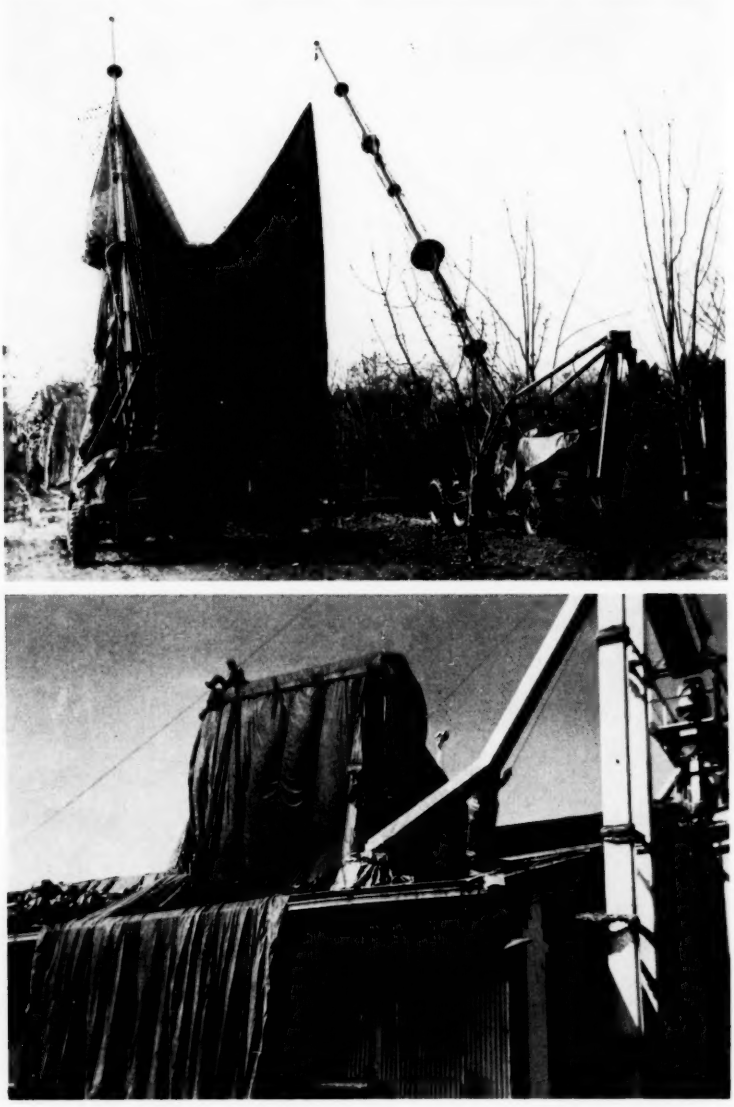

FIG. 7. (above) Hall scale control success was based on gas-tight tents lifted over infested trees by means of tractor-operated booms. (below) Some 145 million cubic feet of granary storage space in California, Arizona, and New Mexico have been fumigated since 1954 for the control of the khapra beetle. (Photos courtesy of the United States Department of Agriculture.)

A few early entomologists, however, thought the Cotton States and Federal Government should attempt to retard the spread of, if not eradicate, the boll weevil. Those who spoke out in favor of positive action, such as Newell, Ball, and others in this period, were considered visionaries. Ball (9) had this to say,

> . . . if the Nation would store cotton in advance, and cease to grow the crop for a single year, its (the boll weevil) eradication might be accomplished. It would even be possible to divide the country into three districts; increase production in one area, eliminate it for two seasons in the other. In this way, it could be more certainly eliminated and cotton still produced.

The pink bollworm, an insect of Old World origin, was first found in east Texas in 1917; in western Louisiana in 1918. It is second only to the boll weevil as a destructive cotton pest. Where both occur, the damage by one is practically added to that of the other. "This insect," according to Hinds (2), "might eliminate the United States from its dominant position in the production of cotton."

The pink bollworm is now recognized as the world's most damaging insect to cotton. The joint Federal-State effort to contain this insect has been continuous since its discovery in the United States. In reporting on early accomplishments against this pest, Hinds (2) said,

> Pink bollworm infestations were eradicated by the most painstaking cleaning up and burning of all cotton stalks, fallen bolls, lint, and seed in infested fields. Every shipment of seed from infested areas was traced. Widespread scouting was continued for several years. Noncotton zones were maintained for 3 years. By strict regulation of adjacent areas, and heat-disinfestation of seed, compressing of lint, etc., these and other infestations found later in central Texas were finally eradicated.

Some 35 years after its discovery in this country, infestations of the pink bollworm still were limited in 1952 to south and central Texas (see Fig. 6). In 1953–54, however, mild winters contributed to an alarming build-up in the number of pink bollworms overwintering in the southern and central parts of Texas. Infestations since then have become established in northeastern Texas, western Arkansas, and Oklahoma, further increasing the threat to the Delta area and Southeastern States. Even so, the pink bollworm has not advanced to the Mississippi River after nearly 40 years in this country. No infestations are known to exist on the West Coast.

Clarification of Federal-State Responsibility

The period from 1916 until the end of World War II was marked with indecision as to the responsibility of the United States Government in dealing with introduced pests. The Mexican bean beetle, as indicated above, was first reported in the eastern United States in 1920. No organized effort was made to suppress or contain it. The European corn borer quarantine was revoked in 1933 and serious consideration was given to curtailing federal assistance in connection with the Japanese beetle program. The imported fire ant, *Solenopsis saevissima* v. *richteri* Forel, occurred for many years in

a small area around the port of Mobile, Alabama. There was no organized effort to stamp it out or to retard its spread in the belief that treatments available for individual use made living with it a fairly simple matter.

There is strong evidence that we have been slow to marshal our forces into a balanced and coordinated program of quarantine, eradication and control. Control effort often has been delayed until a pest has demonstrated its destructiveness. New introductions have become firmly established before any action was taken. Technical information upon which to plan eradication was lacking in many instances. Entomologists have differed in their views as to what types of situations warranted expenditure of public funds. It has been clearly demonstrated time and again that delay in initiating a regulatory program reduces the chances of success and adds to the ultimate cost.

An important step toward clarifying the responsibility of the Federal Government in pest-control programs was made in September 1951 when Charles F. Brannan, then Secretary of Agriculture, appointed a nonpartisan group representing various fields of interest to study Federal-State cooperative regulatory and control programs in pest control. In their report to the Secretary, the Committee stated in part:

> 1. Over-all efforts to eradicate or suppress insects and plant diseases should be continued and intensified. 2. Costs of control measures should be distributed among Federal, State, and local agencies and individual operators, with the Federal Government providing over-all direction and coordination of programs of regional or national concern. 3. Each program should be reappraised periodically to determine whether eradication is possible and if the most effective means of control are being utilized . . .

In 1955, Ezra Taft Benson, Secretary of Agriculture, requested the National Association of Commissioners, Secretaries, and Directors of Agriculture to make a study of federal-state relationships in dealing with crop pest-control problems. This group, which comprised the Executive Committee of the Association, distinguished (*a*) federal, (*b*) state and local, and (*c*) joint responsibilities. They gave the following as examples of federal responsibilities:

> 1. Preventing the introduction of seriously injurious pests of agriculture into the United States. 2. Preventing the spread of seriously injurious pests of agriculture between the States. 3. Developing, correlating, and evaluating pest information from foreign sources. 4. Cooperating with foreign countries, particularly neighboring countries in the control of crop pests to prevent their introduction into the United States. 5. Conducting pest eradication or control programs on Federal property.

The following were examples of responsibilities in the field of pest control that are primarily state:

> 1. Preventing the spread of seriously injurious pests of agriculture by the use of quarantines or other suitable means in the absence of Federal action. 2. Developing and administering intrastate quarantines including those which supplement interstate quarantines. 3. Providing independently or in cooperation with other States for the control of native or naturalized destructive pests normally having reached the limit of their range in this country.

The following were examples of joint responsibilities in the field of pest control:

1. Eradicating or controlling an incipient infestation of a pest new to the United States. 2. Developing and administering programs designed to suppress or prevent interstate spread of pests new to, or not widely distributed in, this country. 3. Eradicating or controlling an unforeseen emergency outbreak of major significance of a pest for which no control program has been provided. 4. Eradicating or controlling an emergency outbreak of a pest against which a control program is in progress, but which has developed in intensity and magnitude substantially beyond expectations and threatens significant losses, or will require larger expenditures at some future date if prompt action is not taken. 5. Correlating data as a guide for development of research. 6. Providing for pest surveys to determine and record the presence of pests and the extent of spread, with particular attention being given to new or potentially serious pests. 7. Developing information for dissemination to the public on the characteristics of important pests and the procedures that are available for suppression or eradication.

Current Status of Eradication Programs in the United States

An organized effort against a destructive foreign pest may have any one of three broad objectives: (*a*) prompt eradication of an incipient infestation; (*b*) containment or suppression of such a pest thus obtaining time for research to develop new procedures which later may lead to an effective eradication program, or, if eradication is not feasible, then research may develop suitable controls should it become necessary to live with the pest; and (*c*) retardation of the spread of a pest limited in its distribution to a small part of its ecological range in this country by protecting uninfested portions from infested host materials that might otherwise move in commerce. The United States government at this writing is participating with the states in a number of programs that fall in each of these categories.

Mediterranean fruit fly.—Eradication of the Mediterranean fruit fly which gained a foothold in Florida for the second time in 1956, is practically assured. From the point of introduction in suburban areas of Miami, the fly spread throughout the southern part of the State and as far north as Orange County. Incipient infestations were detected and eradicated in 28 different counties. More than 600,000 acres were under treatment at one time. The cost of this eradication effort is approximately ten million dollars. The work is jointly financed with the State of Florida, the Federal Government assuming about 50 per cent of the over-all cost.

The Florida State Plant Board estimated that to live with the Mediterranean fruit fly would cost citrus growers and processors approximately 20 million dollars a year. This estimate did not take into account losses to the consumer or damage to other favored hosts, among which are a number of our more cherished soft fruits and certain vegetables.

Khapra beetle.—The khapra beetle, *Trogoderma granarium* Everts, first reported from California in 1953, later was found to infest some 479 establishments involving in excess of 145 million cubic feet of storage space, in the states of Arizona, California, and New Mexico, and the Republic of

Mexico (Fig. 7). The khapra beetle is recognized world-wide as one of the most destructive pests of stored grains and seeds. In a period of three years, and at a cost of about five million dollars, this insect has been suppressed to the point that eventual eradication is a distinct possibility. It would be most difficult to measure in a monetary way the damage this pest would do if it became distributed throughout the grain storage facilities of this country.

Hall scale.—It has taken many years of continuous effort to devise and put into practice procedures which are making possible the eradication of the Hall scale, *Nilotaspis halli* Green. This insect was first reported at Chico, California in 1934 and later found infesting small areas in Butte and Yolo Counties, California. The Hall scale has proved extremely difficult to control. Only by fumigating host trees under gas-tight tents with a high concentration of hydrocyanic acid gas has it been possible to gain the upper hand in dealing with this pest. (Fig. 7). The last living scales were found in the spring of 1956. Only small areas are scheduled for treatment in the fall of 1957, when all infested host plants will have received three fumigations since the last living scales were seen.

Mexican fruit fly—Mexican blackfly.—Through continuous effort the Mexican fruit fly, *Anastrepha ludens* (Loew), and the citrus blackfly, *Aleurocanthus woglumi* Ashby, have been kept out of the citrus areas of this country. This has required vigilance on the part of port-of-entry inspectors and the prompt treatment of incipient infestations as they have appeared in the United States. There has been the closest cooperation with the Mexican government in these operations.

Gypsy moth.—Earlier mention was made of the gypsy moth, introduced into this country more than 80 years ago. Until DDT became available and equipment perfected for the aerial application of liquid insecticides, the gypsy-moth program was primarily a delaying action. However, since World War II, outlying infestations on more than 3,700,000 acres have been eradicated in Michigan, Pennsylvania, and New Jersey. An aggressive holding program is continuing in New York, while in the area of general infestation some ten million acres have been sprayed during the past five years to prevent widespread defoliation and the resulting damage to our forests, parks, and other recreational areas.

The gypsy moth can be eliminated from any given area with a single application of one pound or less of DDT applied per acre as an oil solution. The next few years will determine whether it is possible to push back the western periphery of the infested area. If so, eventual eradication should be the objective.

Should the gypsy moth be permitted to invade the hardwood forests of the southern Appalachians and the Ozarks, it might well find an environment much more to its liking than New England, which is close to the northern limits of its ecological range.

Other programs.—The outlook in regard to certain other programs is not so encouraging. After many years of persistent effort we have procedures

which may be used in the eradication or elimination of outlying infestations of the Japanese beetle. The area of general infestation, however, involves about 6½ per cent of the land area of the United States and opinions vary as to the practicability of achieving more than a holding program. This approach is being taken in such peripheral states as North Carolina, Kentucky, Ohio, Indiana, Michigan, and Missouri with the full realization that natural spread will catch up with them one day unless there is a more aggressive approach to the entire problem.

Treatments are now available which could be employed effectively in a white-fringed beetle eradication program. Our present major weakness in this program is survey. A reliable means of detecting a low population of white-fringed beetles has not been found. Here again, however, quarantine, supported with the application of soil treatments where isolated infestations occur, has served to hold this pest in check. The savings resulting from a successful eradication program would be enormous. Years of research indicate that the white-fringed beetle would undoubtedly become a major pest of southern agriculture if it were permitted to spread unchecked.

The pink bollworm has been discussed briefly in its relation to the boll weevil story. Eradication is out of the question in this case. The pest is widely distributed in Mexico, where, as in the case of the Mexican fruit fly and the citrus blackfly, there is a constant source of reinfestation across the international boundary.

It has been possible to eliminate an infestation of the pink bollworm only by the strictest enforcement of a non-cotton zone. Certain cultural and chemical treatments applied on an area-wide basis lower populations well below the economic level, but once the insect is firmly established in a cotton-growing area, these treatments fall short of eradication. As in the case of the white-fringed beetle, however, continuing quarantine and suppressive efforts have kept damage in areas of general infestation to a minimum, and greatly retarded spread to new areas. Failing the desired objective, the dollar and cents value of the work performed can hardly be questioned.

There is widespread demand in the South for a program aimed at the eradication of the imported fire ant. A large-scale experimental effort, conducted in cooperation with the Dutch Government, led to the eradication of the screwworm, *Callitroga hominivorax* Coquerel, on the Island of Curacao. There is now widespread interest among livestock men of the southeastern part of the United States in an organized area-wide eradication effort utilizing similar procedures.

International Plant Protection Activities

Countries throughout the world have become more aware within the past few years that prevention of the spread of plant pests can best be accomplished by nations working together. The programs of the Food and Agriculture Organization (FAO) of the United Nations are designed to strengthen national activities and to promote international cooperation. It is realized that plant disease and pest problems are mostly international or

regional in nature, and that to build up a common defense among countries, there must be an effective organization of national services.

The International Plant Protection Convention represents an effort of FAO member nations to promote cooperation among themselves in combating plant pests and disease which reduce production of crops produced by at least 20 per cent annually. Many of the more important pests and diseases are not confined to one country. Combined efforts are needed, therefore, to prevent such pests from inflicting heavy losses. Other pests still restricted in distribution are a potential threat to every country of the world.

The need for such a convention to strengthen international action and to replace the obsolete "Convention internationale pour la protection du vegetaux" of 1929, and the "Phylloxera Convention" of 1881, first came before the Food and Agriculture Organization at its Fifth Conference in 1949. In accordance with the recommendation of that Session, FAO presented a draft to all member governments for comments, and also to several technical groups for consideration. The draft, thus several times revised, was approved by FAO at its Sixth Session in 1951. It now has been signed by 37 governments and adhered to by a number of others. Thirty-one governments, including both signatories that ratified it and adhering members, have now become parties to this convention.

In accordance with the Convention, FAO has the responsibility of administering procedural matters and is charged with the implementation of certain technical provisions. Progress has been made along the following lines:

World Reporting Service.—A world-wide reporting service was organized by FAO in cooperation with contracting governments for circulating information on the incidence of plant pests and diseases of economic importance, on the degree of damage they cause, and on their control. The service came into operation in October 1952, with the initiation of a monthly periodical entitled *Food and Agriculture Organization Plant Protection Bulletin.*

Plant Quarantine.—The Convention provides for uniform regulatory and quarantine procedures and a model phytosanitary certificate in order to remedy the diverse restrictions and requirements imposed by different countries governing the importation of plant materials. To facilitate the exchange of information on quarantine legislation and better understanding among governments on this subject, a *Digest of Plant Quarantine Regulations* was issued in 1952. Several supplements have followed. Current changes in quarantine legislation are also reviewed monthly in the *Food and Agriculture Organization Plant Protection Bulletin.*

Development of Regional Organizations.—The Convention provides for the establishment of regional plant protection organizations as coordinating bodies in appropriate geographic regions. Of such regional bodies the most firmly established is the European and Mediterranean Plant Protection Organization (EPPO) with headquarters in Paris. This is a continuation of the International Committee for the Control of the Colorado Beetle. Al-

though EPPO was organized before the International Plant Protection Convention came into existence, it now functions as a recognized regional organization under the Convention.

In Central America and Mexico the international committee originally established for cooperation in locust control, Cómite Internacional Coordinadoro de Lucha Antiacridida (CICLA), is now incorporated into the Organismo Internacional Regional de Sanidad Agropecuria (OIRSA) which covers the entire field of plant protection. Following the conclusion of an agreement in 1953 by governments of Central America and Mexico, with support of FAO, OIRSA came into existence in July, 1955. This regional agency assumes all responsibility in undertaking and coordinating investigations and control operations in the fields of plant protection and animal health.

South American governments from Bolivia south have, for some time, been collaborating in an organization for the control of locusts, Cómite Interamericano Permanente Antiacridiano (CIPA). There is also a Convenio Interamericano de Sanidad Vegetal, whose members are Brazil, Argentina, Paraguay, and Uruguay, covering the control of all other pests. It is believed that these activities may serve as the basis for the establishment of a regional plant protection organization for South America.

At the request of the governments of South East Asia and the Pacific region concerned, a meeting convened in Singapore in 1954, to formulate a plant protection agreement for the purpose of preventing the invasion of dangerous plant diseases and pests from outside the region. The agreement was approved by the FAO Council in November 1955, and signed by countries in the region in December 1956. This established the Plant Protection Committee for the South East Asia and Pacific Region. The Committee has broad powers for advising on plant protection policies and requirements in that section of the world.

From time to time FAO calls meetings of these various committees, which report on progress achieved, propose changes for improvements, and discuss other aspects of plant protection.

In addition to providing for international cooperation in controlling pests and diseases of plants and plant products and in preventing their introduction and spread across international borders, the Convention outlines the policies under which import restrictions for plant protection (phytosanitary) reasons can be justified, and describes the type of national organization each government should provide so far as possible. It outlines procedures for the settlement of disputes, and prescribes a standard form for plant protection (phytosanitary) certificates.

Contracting governments agree to make provisions for (*a*) a competent official plant protection organization, (*b*) distribution of information within the country regarding pests and diseases of plants, (*c*) research and investigation in the field of plant protection, and (*d*) the issuance of phytosanitary certificates. The Convention recognizes the need for the establishment of necessary quarantines by contracting governments to prevent the introduc-

tion and spread of plant diseases and pests. It further provides that each contracting government agrees to report on the occurrence, outbreak, and spread of economically important pests and diseases of plants and plant products that may be of immediate or potential danger; to supply information on effective means to control pests and diseases of plant products; and to cooperate, so far as practicable, in combating destructive pests or diseases which may seriously threaten crop production when international action is needed to meet the emergencies.

Conclusions

There is a growing awareness the world over of the important place that the control of pests such as insects, plant-disease organisms and nematodes have in the broad field of agriculture.

Entomologists engaged in planning and directing large-scale pest control programs are keenly aware of the pitfalls associated with such operations. They recognize the importance of taking full advantage of cultural practices in keeping pests under control. They constantly seek opportunities to utilize microbial pathogens, parasites, and predators in achieving their objectives.

Cultural control must be taken into account in relation to conservation and soil building practices. This may introduce limitations that must be offset by other means. In appraising the value of biological control we must keep in mind that the consuming public in America has come to expect quality standards that do not permit 5, 10, or 20 per cent insect damage. The mass production and release of parasites offer real promise in dealing with certain insects—and this approach to pest control should receive intensive and continuous study. When situations demand use of chemicals, we must take into account residues in relation to both harvested crops and the soils upon which the crops are produced.

No matter what our approach may be in solving insect problems, whether cultural, biological, or chemical, the application of accepted practices on an area-wide basis will always produce most satisfactory results. Our experiences over the past 75 years leave little doubt that the expression "It is better to live without than to learn to live with destructive insects" is sound.

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THE CHEMISTRY AND ACTION OF ACARICIDES[1]

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This review is concerned with those pesticides which are primarily effective against members of the order Acarina, particularly phytophagous mites, at dosages which are largely ineffective against insects. Such pesticides may be termed specific acaricides to distinguish them from insecticides and from other compounds such as the organophosphorus compounds which possess both insecticidal and acaricidal activities. As used in this review, the term "acaricide" includes compounds effective against either the egg stage or active stages or both and the term "action" will be considered in its broadest sense rather than in the more limited sense of the primary biochemical or physiological action on a specific system resulting in a toxic effect.

Although no comprehensive reviews as such have been published on this subject within the past few years, the attention of the reader is directed to the review by Kirby & Tew (1) on agricultural acaricides affecting phytophagous mites and the chapter on acaricides in the book by Metcalf (2) on the chemistry and mode of action of organic insecticides. Information pertinent to the chemistry and action of acaricides is to be found as well in the *Guide to Chemicals Used in Crop Protection* by Martin (3) and the book by Gunther & Blinn (4) on analysis of insecticides and acaricides. Additional information may be found in the recent review on agricultural pesticides by Fischer (5).

CHEMICAL AND BIOLOGICAL PROPERTIES OF ACARICIDES

The acaricides on which information is comparatively less complete in the five review references noted above, or on which extensive new information is available, are discussed in detail below. Only recent additions to the literature are cited for others and in the cases of a few acaricides there has been no recently published information.

Aramite

Chemistry.—Aramite, 2-(*p-tert.*-butylphenoxy)-1-methylethyl 2-chloroethyl sulfite, is hydrolyzed under strongly alkaline conditions to liberate ethylene oxide, on the determination of which Gunther *et al.* (6) have based a very sensitive but complicated microanalytical method. A simpler and more rapid modification has recently been reported by Brokke, Kiigemagi & Terriere (7). The liberated ethylene oxide is converted in acid solution to ethylene glycol which is then cleaved with periodic acid to produce formaldehyde. The formaldehyde is conjugated with phenylhydrazine and treated with sulfuric acid in the presence of periodic acid to form a brilliant red color which is measured spectrophotometrically at 520 mμ.

[1] The survey of literature pertaining to this review was completed in June, 1957.

Under strongly acid conditions on the other hand Aramite is hydrolyzed to liberate SO_2 which has been utilized by Watson (8) for the development of a new analytical method. The liberated SO_2 is swept with a stream of inert gas to a special indicator paper containing sodium nitroprusside, zinc sulfate, and ammonia. In the presence of SO_2 a red-colored complex is formed which can be quantitatively compared with standards.

Butoxy Polypropylene Glycol

This compound is best known for its activity as a fly repellent [Granett *et al.* (9)]. It has nevertheless shown promise in laboratory and limited field trials as a spray for phytophagous mites showing toxicity to the active stages but no pronounced ovicidal action [Haynes *et al.* (10); Armstrong (11)].

Chemistry.—Butoxy polypropylene glycol is a colorless liquid polymer which can be produced in various fractions of increasing mean molecular weights. The fraction having a mean molecular weight of 800 has the following properties: vapor pressure 1×10^{-8} mm. Hg. at 30°C., flash point approximately 420°F., specific gravity 0.990 at 20°/20°C., average weight 8.25 lbs./gal. at 20°C., and viscosity 250 Saybolt sec. at 100°F. [Granett *et al.* (9)]. It may be prepared by the following reaction [Fife & Roberts (12)]:

$$CH_3CH\!-\!CH_2 \;(\text{O}) + C_4H_9OH \xrightarrow[NaOC_4H_9]{N_2} C_4H_9(OCHCH_2)_xOH \quad (CH_3)$$

Butoxy polypropylene glycol (800) is relatively insoluble in water; 0.1 per cent will dissolve at 20°C. However, it will dissolve 4.5 per cent of its own weight of water at this temperature. The compound is miscible with the common aliphatic and aromatic hydrocarbon solvents such as deodorized kerosene and methylated naphthalenes. It is an excellent solvent itself for many of the common insecticides [Carbide and Carbon Chemicals Co. (13)]. The compound is thermochemically stable at 500°F. and is resistant to oxidation. It does not corrode metals or swell rubber and was originally suggested for use as a lubricant or brake fluid [Fife & Roberts (12)].

Relation of structure to activity.—There is almost no published information on the relation of structure to activity. Wellman & McNamee (14) indicate that a fraction of approximately 100 Saybolt sec. viscosity is preferred for fly repellent action and one of 200 to 450 for acaricidal activity.

Toxicology.—The acute oral LD_{50} is 9.1 gm./kg. for the rat and 23.9 gm./kg. for the rabbit. Lethal single doses produce hyperexcitability of the central nervous system. A single dose of 20 ml./kg. in a skin absorption trial killed one of ten rabbits. A 90-day inunction trial on rabbits of 1 gm./kg./day caused no injury beyond early transient erythema and desquamation. No primary skin irritation or sensitization was produced by skin patch tests on 200 persons [Shaffer *et al.* (15); Carpenter *et al.* (16); Haynes *et al.* (10)].

Chlorbenside

This compound is characterized by activity against mite eggs and larvae but not the adults. It shows the ability to penetrate across and diffuse

through leaves as do certain of the substituted benzene sulfonates [Cranham, Higgons & Stevenson (17); Cranham & Stevenson (18)].

Chemistry.—Chlorbenside, *p*-chlorobenzyl *p*-chlorophenyl sulfide, is a white odorless crystalline solid, m.p. 72°C. and vapor pressure 6.1×10^{-5} mm. Hg. at 40°C. It may be prepared by the following reaction [Greenwood & Stevenson (19)]:

$$p\text{-}ClC_6H_4CH_2Cl + p\text{-}ClC_6H_4SNa \rightarrow p\text{-}ClC_6H_4CH_2SC_6H_4\text{-}p\text{-}Cl + NaCl$$

Chlorbenside is practically insoluble in water, of low solubility in alcohols and petroleum oils and readily soluble in acetone and aromatic hydrocarbons. Higgons & Kilbey (21) have characterized technical Chlorbenside, containing 90 per cent or more of the primary compound, and they have found up to the following percentages of impurities: *o*-chlorobenzyl *p*-chlorophenyl sulfide, 5 per cent; *m*-chlorobenzyl *p*-chlorophenyl sulfide, 2.5 per cent; 2,4-dichlorobenzyl *p*-chlorophenyl sulfide, trace; *p*-chlorobenzaldehyde, 2 per cent; bis-*p*-chlorophenyl disulfide, 1 per cent; *p*-chlorobenzaldehyde di-*p*-chlorophenyl mercaptal, 1 per cent; and *p*-chlorobenzilidene chloride, 1 per cent.

Chlorbenside is very inert to most types of chemical reactions including reduction and acid and alkaline hydrolysis but can readily be oxidized to *p*-chlorobenzyl *p*-chlorophenyl sulfoxide, m.p. 124°C., and under more strenuous conditions to *p*-chlorobenzyl *p*-chlorophenyl sulfone, m.p. 148°C. Higgons & Kilbey (20) have extensively studied the possible reactions of aryl sulfides of this type and have concluded that only the oxidative reactions show any possibility of use for analytical techniques. Two types of color reactions are possible with *p*-chlorobenzyl *p*-chlorophenyl sulfone: (*a*) nitration to the trinitro derivative, m.p. 222°C., which reacts in benzene with 10 per cent $NaOCH_3$ to give a purple color and (*b*) condensation of the methylene group, activated by the presence of the two sulfone oxygens, with *m*-dinitrobenzene. Further studies [Higgons & Kilbey (21)] have shown that the trinitro derivative gives a red-colored product with analine, reacts in acetone solution with alkali to give a light orange color, and after reduction of the NO_2 groups and diazotization, gives a series of colors with a variety of coupling agents.

Watson (22) found that ultraviolet absorption at 262 mμ offered a rapid method of analysis for technical and formulated samples after appropriate extraction and cleanup. Gunther, Blinn & Barnes (23) have reported that it is possible to distinguish the sulfide, sulfoxide, and sulfone by their infrared spectra. All three compounds absorb strongly in the 1095 to 1085 $cm.^{-1}$ region; the sulfone at 1155 $cm.^{-1}$; and sulfoxide at 1055 $cm.^{-1}$. They were able to separate the sulfide, sulfoxide, and sulfone by selective adsorption on Attaclay but were unable to elute the sulfoxide. Studies of residues on pears utilizing these techniques demonstrated the presence of the sulfone in plant tissues confirming the observation of Cranham, Higgons & Stevenson (17), who reported the presence of the sulfoxide and sulfone on leaves.

Relation of structure to activity.—Both the sulfoxide and sulfone deriva-

tives are reported to have the same degree of biological activity but not the penetrative properties of the parent compound. Little additional information on the relation of structure to activity has appeared except that the benzyl phenyl sulfide exhibits little activity [Cranham, Higgons & Stevenson (17)].

The discovery of Chlorbenside followed investigation of the bridge between two benzene nuclei after it was found that 1,2-bis(phenylthio)ethane and bis(phenylthio)methane possessed considerable acaricidal activity. Brookes *et al.* (24) have reported on the activities of an extensive series of α,ω-bisphenylthioalkanes. They found little difference in the methane, ethane, and propane analogues but a sharp decrease in activity for the higher members. Maximum activity was associated with the bis-*p*-chloro and bis-*m*-chloro isomers. Polychloro-, fluoro-, nitro-, amino-, hydroxy-, or acetoxy-substituted compounds showed decreased or slight activity or were inactive. Little activity was found for a few bisalkylthioalkanes and bisheterocyclicthioalkanes and for sulfoxides and sulfones of the bisarylthioalkanes.

Preparations but not biological activities have been reported for *o*-, *m*-, *p*- and polychloro-substituted isomers of benzyl phenyl sulfide [Greenwood *et al.* (25)]; mixed chloro- and fluoro-substituted isomers [Stevenson *et al.* (26)]; *p*-nitrobenzyl *p*-chlorophenyl sulfide [Stevenson *et al.* (27)]; and a number of sulfoxides of the *o*-, *m*-, and *p*-chloro isomers [Stevenson *et al.* (28)].

Toxicology.—The oral LD_{50} to mice is greater than 3 gm./kg. Daily oral doses of 250 mg./kg. to rats for three weeks had no effect on growth or blood picture, but produced moderately enlarged livers without any pathological changes [Metcalf (2)].

Chlorobenzilate

This compound has proved to be effective against all stages of several phytophagous mites [Gasser (29); Armstrong (11); Jeppson, Jesser & Complin (30)] and at least two species of parasitic mites [Gasser & Wyniger (31); Bailey & Carlisle (32)]. Its activity to the fowl tick has been shown as well [Rodriguez & Riehl (33)].

Chemistry.—Chlorobenzilate, ethyl 4,4′-dichlorobenzilate, is a yellowish viscous liquid, b.p. 141–2°C. at 0.06 mm. Hg. The technical product contains approximately 90 per cent of the above compound and is a brown liquid, specific gravity 1.2816 at 20°/4°C. and average weight 10.7 lbs./gal. [Gasser (29); Geigy Agricultural Chemicals (34)]. It may be prepared by the following reaction [Häfliger (35)]:

$$(4\text{-}ClC_6H_4)_2C(OH)COOH + C_2H_5OH \rightarrow (4\text{-}ClC_6H_4)_2C(OH)COOC_2H_5$$

Chlorobenzilate is practically insoluble in water but soluble in the common organic solvents. Benzene, acetone, methyl alcohol, and deodorized kerosene all dissolve Chlorobenzilate in excess of 40 per cent.

The compound is readily hydrolyzed by alkali and strong acid to 4,4′-dichlorobenzilic acid and ethanol. The ready hydrolysis of Chlorobenzilate is utilized for clean-up purposes in analytical methods by selective extraction procedures. Blinn, Gunther & Kolbezen (36) hydrolyzed Chlorobenzilate and

then selectively oxidized the benzilic acid derivative to 4,4′-dichlorobenzophenone. The ketone was determined by absorption at 264 mμ or by absorption of its 2,4-dinitrophenylhydrazone in alcoholic alkali at 510 mμ. Harris (37) nitrated Chlorobenzilate and treated the nitrated product with sodium methylate to produce a red-colored complex, measured spectrophotometrically at 538 mμ. The method is applicable in the presence of DDT by saponification of Chlorobenzilate to the benzilic acid derivative and selective extraction of DDT and DDE and the acid. The nitrated acid gives the same red-colored complex as the ester.

Relation of structure to activity.—Although no direct information has been published on the comparative acaricidal activities of analogues and homologues of Chlorobenzilate, it may be implied from the patent [Häfliger (35)] that the bis-*p*-chlorophenyl structure is more active than structures with other ring substituents; that alkyl esters are more effective than alkenyl, haloalkyl, alkoxyalkyl, cycloalkyl, or cycloalkenyl esters; and that the ethyl ester is more active than the *n*-propyl or *iso*-propyl esters. The closely related compound, 1-ethoxymethyl-1,1-bis(*p*-chlorophenyl) carbinol, in which the carboethoxy group of Chlorobenzilate is replaced with an ethoxymethyl group, possessed about the same degree of acaricidal activity as Chlorobenzilate in laboratory trials [Gasser (29); Häfliger (38)] but was somewhat less effective in field trials [Armstrong (11)].

Toxicology.—The acute oral LD_{50} for the pure compound is reported by Gasser (29) to be 4850 mg./kg. for the mouse and 3100 mg./kg. for the rat. Horn, Bruce & Paynter (39) found the acute oral LD_{50} of the technical compound to be slightly greater than 700 mg./kg. for both the mouse and rat. A two-year chronic feeding study with rats indicated that the maximum tolerated dietary level is approximately 500 p.p.m. No significant differences in mortality or in gross or microscopic pathology were observed between the experimental animals and the controls. Dogs tolerated 64.1 mg./kg./day for 35 weeks without signs of toxicity or gross and microscopic pathology. Metabolism studies with dogs and rats indicated that the bis(*p*-chlorophenyl) methyl portion of Chlorobenzilate is rapidly excreted in the urine and that there is no significant storage in the tissues.

Dimite

Chemistry.—Losco, Speroni & Peri (40) have reported an additional chemical preparation for Dimite, bis(*p*-chlorophenyl)methyl carbinol, as shown by the following reaction:

$$C_6H_5Cl + Br_2 \xrightarrow[Fe]{} 4\text{-}ClC_6H_4Br + Mg \rightarrow 4\text{-}ClC_6H_4MgBr$$
$$+ CH_3COOC_2H_5 \rightarrow (4\text{-}ClC_6H_4)_2C(CH_3)OH$$

Although nothing is known of the metabolism of Dimite in mites, Perry, Mattson & Buckner (41) have shown that it is rapidly metabolized and excreted as bis(*p*-chlorophenyl) acetic acid in DDT-resistant house flies. Bis(*p*-chlorophenyl) ethylene was postulated as being an intermediate product of

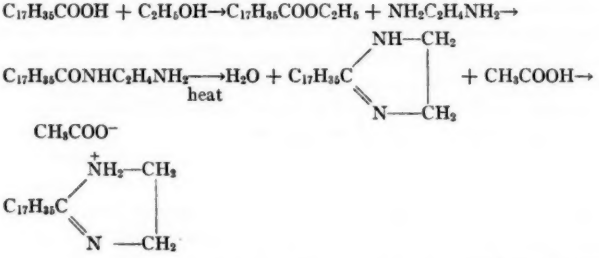
metabolism. It may be possible that rapid detoxication is responsible for its low activity toward insects. Moorefield & Kearns (42) have demonstrated *in vitro* that Dimite has a marked and constant inhibitory effect through a wide range of concentrations on DDT-dehydrochlorinase from DDT-resistant house flies and that DDT-dehydrochlorinase has no metabolizing effect on Dimite.

Relation of structure to activity.—Gunther, Blinn & Metcalf (43) have examined the structure-toxicity relationships of a number of topographical analogues of Dimite. They found that the aromatic substituents had a pronounced effect on acaricidal activity in the approximate order: *p,p'*-dichloro > *p*-chloro-*p'*-hydrogen > *p*-chloro-*p'*-methyl > *p,p'*-dimethyl > unsubstituted > *p*-methyl-*p'*-hydrogen. With substitutions in the aliphatic portion of the molecule, the differences in activity appeared to be in the order trichloromethyl > methyl > dichloromethyl > ethyl > isopropyl. Activity data indicated that both the aromatic and aliphatic moieties of the molecule are important and interdependent in exerting total biological action.

Glyodin

Glyodin had its early development as a fungicide [Wellman & McCallan (44); Thurston *et al.* (45)] but it was soon noted that field applications for apple scab had a definite suppressing effect on the build up of European red mite, *Metatetranychus ulmi* (Koch) [Chandler & Thurston (46); Hilborn & Lathrop (47); Armstrong (11); Clancy & McAlister (48)].

Chemistry.—Glyodin, 2-heptadecyl glyoxalidine acetate, is a light orange odorless crystalline solid, m.p. 62°–68°C., and density 1.035 gm./ml. at 20°C. The free base is a soft waxy solid, m.p. 94°C. It may be prepared according to the following reaction [Kiff (49)]:



Preparations from commercial stearic acid which contains palmitic and oleic acids, give 2-pentadecylglyoxalidine, m.p. 98°C., and 2-(8-heptadecenyl) glyoxalidine, m.p. 52°C., as impurities in the final product. Diamides of the acids may also be formed but can readily be removed by selective extraction.

Glyodin is practically insoluble in water, acetone, and toluene; partially soluble in solvents such as propylene glycol and ethylene dichloride; and soluble in isopropanol to the extent of 39 per cent [Anonymous (50)]. It is subject to hydrolysis to the monostearamide, $C_{17}H_{35}CONHC_2H_4NH_2$, in

which form some or all of the residues on treated products may be found. Both glyodin and the monostearamide are cationic surface-active agents, and Hillenbrand, Sutherland & Hogsett (51) utilized this property in the development of an analytical method. The method involves the titration of the glyoxalidines and their hydrolysis products with a standard solution of an anionic surface-active agent, dioctyl sodium sulfosuccinate, in a two-phase system, chloroform-water, using methylene blue for an indicator. The methylene blue, which at the start of the titration concentrates in the water layer, forms a chloroform-soluble complex with the anionic reagent when the equivalence point is reached, resulting in the migration of the blue color to the chloroform layer. An improved method [Carbide and Carbon Chemicals Co. (52)] utilizes this same property and a two-phase (chloroform-water) system containing 5′,5″-dibromo-*o*-cresolsulfonephthalein (bromcresol purple) indicator. The color complex formed is quantitatively extracted into the chloroform and spectrophotometrically measured at 410 mμ.

Relation of structure to activity.—There is no published information on the relation of structure to acaricidal activity.

Toxicology.—The acute oral LD_{50} is 5.77 gm./kg. for the rat. In its pure form it is irritating to rabbit skin and has some sensitizing action on the human skin after prolonged contact, but dilute suspensions or solutions irritate little if at all. Pure glyodin will produce chemical burns of the rabbit eye but effects from the standard formulation used for agricultural purposes are minor (50).

Karathane

Karathane is another compound showing unusual activity both as a fungicide, especially against powdery mildews, and as an acaricide against a number of phytophagous mites [Rich & Horsfall (53); Lathrop & Hilborn (54); McClellan & Smith (55); Armstrong (11)].

Chemistry.—Karathane, 2-(1-methylheptyl)-4,6-dinitrophenyl crotonate, is a viscous liquid, b.p. 138°–40°C. at 0.05 mm. Hg. It can be prepared according to the following reaction [Hester & Craig (56)]:

$$2\text{-}C_6H_{13}CH(CH_3)C_6H_4OH + HNO_3 \rightarrow 2\text{-}C_6H_{13}CH(CH_3)\text{-}4,6\text{-}(NO_2)_2C_6H_2OH$$

$$+ CH_3CH = CHCOCl \xrightarrow[\text{amine}]{\text{tertiary}} CH_3CH = CHCOOC_6H_2\text{-}4,6\text{-}(NO_2)_2\text{-}2\text{-}CH(CH_3)C_6H_{13}$$

Karathane is insoluble in water, soluble in most common organic solvents, but has limited solubility in alcohol.

The compound can readily be hydrolyzed to dinitrocaprylphenol and crotonic acid. Rich & Horsfall (53) showed in laboratory tests that the residual activity and phytotoxicity (and undoubtedly the acaricidal activity) of Karathane are due to the substituted phenol portion of the molecule and the fungitoxicity to the crotonic acid portion. Deposits on glass slides showed fungitoxic action before drying but not after, due to hydrolysis and loss of crotinic acid by volatilization. Drying on a leaf surface reasonably maintained activity.

Since hydrolysis is the most likely decomposition route, a residue method for the determination of dinitrocaprylphenol has been worked out by Stanley *et al.* (57). Karathane and its dinitrocaprylphenol decomposition product are suitably extracted and taken up in a pyridine-water reagent. After hydrolysis of any intact Karathane, the absorbance of the yellow-colored solution is measured at 422 mμ.

Relation of structure to activity.—Although there is no specific published information on the relation of structure to activity for substituted phenyl crotonates, the relationship of structure of phenols to activity is well known and has been reviewed by Metcalf (2).

Toxicology.—The acute oral LD_{50}'s for the rat are 980 mg./kg. (male) and 1190 mg./kg. (female). The acute oral LD_{50} for the 25 per cent wettable powder for the rat is 8 gm./kg. [Craig (58)].

Kelthane

Kelthane is one of the newer organic acaricides and is characterized by activity against both eggs and motile stages of a number of phytophagous mites [Barker & Maughan (59); Garmus & Unger (60); Jefferson & Morishita (61); Jeppson *et al.* (62)].

Chemistry.—Kelthane, 1,1-bis(*p*-chlorophenyl)-2,2,2-trichloroethanol, is a crystalline solid, m.p. 78.5°–79.5°C., b.p. 180°C. at <0.1 mm. Hg [Rosenthal, Frisone & Gunther (63)]. It may be prepared by the following reaction [Craig (58)]:

$$(4\text{-}ClC_6H_4)_2CClCCl_3 \xrightarrow[H^+]{H_2O} (4\text{-}ClC_6H_4)_2C(OH)CCl_3$$

It is practically insoluble in water and soluble in the common organic solvents.

Kelthane is relatively stable to oxidation but under mildly alkaline conditions it undergoes a haloform-type reaction to produce 4,4′-dichlorobenzophenone and chloroform. These chemical characteristics have been utilized as the basis for the development of two analytical methods. Rosenthal, Frisone & Gunther (63) have suitably swept the liberated chloroform from extraneous materials in a special apparatus and by the Fujiwara reaction, in which the chloroform is heated to 100°C. in a pyridine-water-NaOH mixture, produced a red dye (absorption maxima 530 mμ and 369 mμ) which was measured spectrophotometrically at 535 mμ. Gunther & Blinn (64) have developed a direct ultraviolet spectrophotometric method in which the 4,4′-dichlorobenzophenone is measured at 264 mμ or a colorimetric method in which its 2,4-dinitrophenylhydrazone is measured at 510 mμ. In residue applications, chromic anhydride oxidative cleanup of extraneous extractives is recommended and suitable because of the resistance of Kelthane to oxidation.

Relation of structure to activity.—Wilson & Barker (65) have shown that in a series of α-substituted benzhydrols, $Ar_2C(OH)R$, maximum acaricidal activity is obtained when Ar is 4-chlorophenyl, although the compounds where Ar is phenyl or 4-ethylphenyl also show activity. In the series $(4\text{-}ClC_6H_4)_2$

$C(OH)CH_{3-n}Cl_n$, acaricidal activity increases as $_n$ increases from 1 to 3, the trichloro-derivative being the most active. Gunther, Blinn & Metcalf (43) investigated a series of topographical analogues of Dimite, including Kelthane. They found that maximum activity was associated with the bis-*p*-chlorophenyl structure and the trichloromethyl structure of the alkane portion of the carbinol molecule (see also comments under Dimite).

Blinn, Gunther & Metcalf (66) have examined the insecticidal and acaricidal activities of a series of 2,2,2-trichloro-1-aryl-ethanols which may be considered precursors of the DDT- or Kelthane-type molecule. Of the carbinols and their acetates prepared, where the aryl portion was phenyl, *p*-chlorophenyl, *p*-tolyl, thienyl, 5-chlorothienyl, furyl, pyrryl, or N-methyl pyrryl, only the *p*-chlorophenyl carbinol showed toxicity at 0.25 per cent to the citrus red mite, *M. citri*. Further studies on a series of esters and ethers of 2,2,2-trichloro-1-*p*-chlorophenyl ethanol have been reported by Kolbezen *et al.* (67). The 15 esters and ethers examined showed an approximate equal toxicity to the citrus red mite and greenhouse thrips, *Heliothrips haemorrhoidalis* (Bouché). Significant differences in toxicity to the confused flour beetle, *Tribolium confusum* Duval, however suggested that *in situ* hydrolysis to the free carbinol was not necessary for toxicity. In addition, if the free carbinol were the toxic agent, the ethers would not have been toxic. This is a further demonstration that the entire molecule must be considered in relation to biological activity.

Toxicology.—The acute oral LD_{50}'s for technical Kelthane for the rat are 809 ± 33 mg./kg. (male) and 685 ± 16 mg./kg. (female) [Garmus & Unger (60)]. The acute percutaneous LD_{50} for the 25 per cent emulsifiable concentrate is >100 ml./kg. for the rat [Barker & Maughan (59)].

Ovex

Chemistry.—A new analytical method for the determination of ovex, *p*-chlorophenyl *p*-chlorobenzene sulfonate, in orange pulp has been reported by Butzler, Luce & Wing (68). The method depends on the hydrolysis of ovex with alcoholic KOH to *p*-chlorophenol and potassium benzene sulfonate. The *p*-chlorophenol, recovered by steam distillation, is nitrosated, chromatographed, and measured colorimetrically at 430 mμ. The procedure eliminates non-steam-distillable phenolic-like impurities which may cause interference.

Sulphenone

Chemistry.—Technical Sulphenone contains about 80 per cent *p*-chlorophenyl phenyl sulfone, the remainder consisting of bis(*p*-chlorophenyl) sulfone and diphenyl sulfone; small amounts of *o*- and *m*-chlorophenyl phenyl sulfone may also be present. These aryl sulfones undergo the usual ring reactions such as nitration and sulfonation but they are extremely stable toward chemical reagents with respect to the SO_2 group. Reduction, cleavage, and other reactions have been observed but none appear suitable as the basis for an analytical method [Shuman (69)]. Patchett (70) has developed a two-stage analytical method based on chromatography and ultraviolet spectro-

photometric measurements. Sulphenone, bis(*p*-chlorophenyl) sulfone, and diphenyl sulfone are separated from each other and from extraneous plant and animal extractives by chromatography on alumina and synthetic magnesium silicate columns. The separated constituents in three chromatographic fractions are directly measured by their ultraviolet absorptions at three different wave lengths for each fraction.

Relation of structure to activity.—*p*-Bromophenyl phenyl sulfone is only slightly less active than Sulphenone as an acaricide. Diphenyl sulfone or bis(*p*-chlorophenyl) sulfone or their mixtures synergize Sulphenone and its bromo analogue [Bender (71)].

Toxicology.—The oral LD_{50} for a crude material (45 per cent sulphenone) to mice is 2.7 gm./kg. and to rats, 1.4 gm./kg.; for a purified material to mice, 3.65 gm./kg., and to rats, >2 gm./kg. The acute intraperitoneal LD_{50} for the crude material to mice is 1 gm./kg. and to rats about 500 mg./kg. Levels of 1,000 and 10,000 p.p.m. in the diets of rats over a two-year period resulted in a lowering of body weight only in the high-level group. Daily doses of 10, 50, and 100 mg./kg. to dogs over prolonged periods caused non-specific toxicity only at 100 mg./kg. Eye tests on rabbits resulted in transient irritation and repeated skin tests on rabbits and guinea pigs were negative. Sulphenone storage in dog and rat tissues after prolonged oral administration was insignificant. Sulphenone and bis(*p*-chlorophenyl) sulfone were detected in various tissues, the highest quantities being found in fat, but no diphenyl sulfone could be detected, indicating complete excretion of this compound or metabolism to a nondetected component [Hazelton, Kundzins & Bruce (72)].

Tedion

This compound is one of the newer organic acaricides and is characterized by activity against mite eggs, larvae, and nymphs but not adults. It has shown a retarding influence on reproduction in that eggs laid by adult females after contact with a Tedion residue are no longer viable [Huisman, van der Veen & Meltzer (73)].

Chemistry.—Tedion, 2,4,4′,5-tetrachlorodiphenyl sulfone, is a white crystalline solid, m.p. 148°–148.5°C. [N. V. Philips-Roxane (74); Niagara Chemical Division (75)]. The technical product contains 93–95 per cent of the 2,4,4′,5-isomer and may be prepared by the following reaction [Cassil (76)]:

$$2,4,5\text{-}Cl_3C_6H_2SO_2Cl + C_6H_5Cl \xrightarrow[AlCl_3]{} 2,4,5\text{-}Cl_3C_6H_2SO_2C_6H_4\text{-}4\text{-}Cl + HCl$$

Tedion is practically insoluble in water and exhibits limited solubility in the common organic solvents. Solvents such as xylene, dioxane, chloroform, and ethylene dichloride will dissolve from 5 to 15 per cent of technical Tedion at 25°C. [Cassil (76)]. Because of its limited solubility satisfactory emulsifiable concentrates have not been formulated.

Tedion is very stable chemically, being very resistant to acid and alkaline hydrolysis. It can be nitrated with the standard mixture of fuming nitric and sulfuric acids. The nitrated derivative when treated with piperidine and

aqueous KOH yields a red-colored complex which can be measured spectrophotometrically [Cassil (76)].

Relation of structure to activity.—Eaton & Davies (77) found that in a series of substituted diphenyl sulfones, maximum activity was associated with diphenyl sulfone and its mono-*p*-chloro analogue. The di-*p*-chloro compound was significantly less effective. In searching for active compounds of lower phytotoxicity, Huisman *et al.* (73) found that both the 2,4,5-trichloro compound and the 2,4,4′,5-tetrachloro compound showed high acaricidal activity with low phytotoxicity. It is of interest that Kenaga & Hummer (78) found that the related 2,4,5-trichlorophenyl 4-chlorobenzenesulfonate was inactive toward the two-spotted spider mite and Mexican bean beetle larvae.

Toxicology.—The acute oral LD_{50} to mice is >5 gm./kg., at which dosage no visible symptoms were noted and no deaths occurred [Huisman *et al.* (73)]. No mortalities were observed with rats dosed orally by stomach tube with 14.7 gm./kg. Applications for 24 hours of a Tedion methyl cellulose paste to the clipped abdomen of rabbits at a rate of 10 gm./kg. caused only a minor skin irritation which cleared up in one to five days. A single application of 3 mg. instilled into the eye of a rabbit resulted in mild irritation, the animal returning to normal in 24 to 48 hours. Tedion in the diet of mice at 0.4 per cent and rats at 2.0 per cent caused no significant mortality after six months of feeding [Niagara Chemical Division (75)].

Miscellaneous Acaricides

Reports on numerous compounds showing acaricidal activity may be found in the literature, particularly the patent literature. However, only a small fraction of these compounds reach final development as commercial acaricides, such as those discussed above, since many factors including phytotoxicity, formulation, pharmacology, post-harvest residues, production, economics, etc., influence final development in addition to acaricidal activity. The other compounds retain importance nevertheless for the continued study of the relationships of structure to activity and potentially perhaps even more at the present time in relation to the problem of resistance to presently available compounds. Unfortunately, limitations of space prevent a complete discussion and record of these compounds in this review. Many of them are entirely unrelated structurally to the present commercial acaricides, for example, simple compounds such as lithium cyanate [Ter Horst (79)] or more complex molecules like aryl substituted thiadiazoles [Stevenson, Cummings & Cranham (80)]. Others are more closely related to the present commercial acaricides, for example, 2-cyclohexyl-4,6-dinitrophenyl acetate [Bottger, Yerington & Gertler (81); Yerington & Gertler (82)] or 1,4-dioxa-8-*tert*-butylspiro[4,5]decyl-2-methyl 2-chloroethylsulfite [Gatzi & Müller (83)].

BIOLOGICAL ACTIVITY AND SPECIFICITY

The specific acaricides were initially defined as pesticides which are primarily effective against members of the order Acarina, especially phyto-

phagous mites, at dosages which are largely ineffective against insects. In general this is a satisfactory broad definition but one to which there may be a number of exceptions and qualifications.

Insecticidal action of acaricides.—A classic demonstration of the intergrading nature of the relationship of structure to insecticidal and acaricidal activities is that of Metcalf (84) in which changes in the aliphatic portion of the DDT molecule produced a series of compounds of essentially opposite relative orders of effectiveness for acaricidal and insecticidal action. Bis(*p*-chlorophenyl) methane was effective both as an insecticide and an acaricide and was unique in this respect among the compounds examined. Läuger, Martin & Müller (85) found that *p*-chlorophenyl *p*-chlorobenzene sulfonate, *p*-chlorophenyl *p*-chlorobenzyl ether, bis(*p*-chlorophenyl) sulfide, bis(*p*-chlorophenyl) sulfoxide, bis(*p*-chlorophenyl) sulfone, and bis(*p*-chlorophenyl) ether were active as stomach poisons to clothes moth larvae. All of these compounds have since been shown to possess acaricidal activity [Metcalf (84); Eaton & Davies (86); Kenaga & Hummer (78)]. The same toxicity relationships to larvae of the Mexican bean beetle, *Epilachna varivestis* Mulsant, and eggs and adults of the two-spotted spider mite, *Tetranychus telarius* (Linnaeus), have been demonstrated for a series of bis(substituted phenoxy) methanes [Kenaga (87)] and a series of substituted phenyl benzene sulfonates [Kenaga & Hummer (78)].

The toxicity of acaricides to beneficial insects is of practical importance. In general acaricides show moderate to no toxicity to the honey bee, *Apis mellifera* Linnaeus. Atkins & Anderson (88) found Chlorobenzilate, Sulphenone, and Aramite moderately toxic and ovex, Genite, Neotran, and Dimite relatively safe. Beran & Neururer (89) classed Tedion as one of the less toxic materials to bees. Bailey & Carlisle (32) tested a series of acaricides as pyrotechnic smokes and found Chlorobenzilate and Dimite to be less toxic than Chlorbenside and ovex. *p*-Chlorophenyl benzene sulfonate, azobenzene, azoxybenzene and Tedion were the most toxic of the acaricides examined, although Tedion showed little toxicity at doses which were still acaricidal. Aramite and ovex have been shown to be practically non-toxic and Neotran nearly so to three species of entomophagous insects, *Aphytis chrysomphali* (Mercet), *Metaphycus helvolus* (Compere), and *Lindorus lophanthae* (Blaisdell) [Bartlett (90)].

As a group the true acaricides can be considered to be of relatively low toxicity to the insects on which they have been tested. In fact this specificity has been utilized for the selective control of mite pests. Chlorobenzilate and Chlorbenside have been utilized in insect vector virus research for the control of spider mites in the greenhouse without harm to leafhoppers and aphids [Wolfe (91)]. Direct control of the acarine disease of bees caused by the mite *Acarapis woodi* (Rennie) has been accomplished with Chlorobenzilate, Dimite, and ovex [Bailey & Carlisle (32)]. Various parasitic mites in insect cultures have been controlled with Neotran, ovex, Dimite, and Tedion [Sellers & Robinson (92); Baker *et al.* (93); Mulla & Barnes (94)]. The low

toxicity of the true acaricides to warm-blooded animals has facilitated the control of parasitic mites in mouse and rat colonies. Control of the snake mite, *Ophronyssus natricis* (Gervais), has been reported [Baker *et al.* (93)].

Acaricidal specificity.—The specificity of acaricides is not limited to differential toxicity to mites and insects for there are many examples of clearcut specificity in relation to acaricidal activity itself. Chlorobenzilate is more effective than Kelthane in field experiments for the control of the citrus bud mite, *Aceria sheldoni* (Ewing), but just the opposite is true for the citrus flat mite, *Brevipalpus lewisi* (McGregor). Yet Chlorobenzilate is more effective than Dimite, ovex, Sulphenone, or Aramite against the latter species. Kelthane is more effective against the citrus red mite, *Metatetranychus citri* (McGregor), than ovex or Aramite which are in turn more effective than Chlorobenzilate [Jeppson, Jesser & Complin (30); Jeppson *et al.* (62)]. Jefferson & Morishita (61) found that Kelthane gives excellent control of the cyclamen mite, *Steneotarsonemus pallidus* (Banks), against which Chlorobenzilate and Aramite are ineffective. Kelthane and Chlorobenzilate are effective against the privet mite, *Brevipalpus inornatus* (Banks), but Aramite is only moderately effective against this species. Cole & Fisk (95) have examined the toxicity of Dimite and Aramite to the carmine and green forms of the two-spotted spider mite, *T. telarius.* They demonstrated that differences in mite susceptibility may result from different host plants and that relative susceptibility of the color forms may or may not vary with the acaricide.

Acaricidal activity of insecticides.—The chlorinated hydrocarbon insecticides are usually considered to be relatively ineffective against phytophagous mites but again exceptions may be found. DDT and chlordane are effective against the citrus bud mite, *A. sheldoni* [Jeppson (96)]. It seems reasonable that the effectiveness of both DDT and Kelthane to this mite must be interrelated. Endrin and toxaphene are as effective as sulphur, which is the recommended control material, toward the tomato russet mite, *Vasates lycopersici* (Massee), as also are Sulphenone and ovex. Chlordane, heptachlor, aldrin, dieldrin, isodrin, and DDT are nearly as effective as sulphur but Aramite and Dimite are relatively ineffective [Tuft & Anderson (97)]. Before Kelthane was investigated for control of the cyclamen mite, *S. pallidus,* endrin was the most effective control material [Jefferson & Morishita (61)]. DDT and lindane effectively control the red-legged earth mite, *Halotydeus destructor* (Tucker) [Barber & Bath (98)].

The specificity of action of the chlorinated hydrocarbon insecticides against mites involves some additional interesting relationships. Almost immediately after the use of DDT was initiated for the control of certain orchard pests such as the codling moth, *Carpocapsa pomonella* (Linnaeus), it was noted that various *Tetranychus* spp. markedly increased [Steiner, Arnold & Summerland (99); Dean (100); Hough (101); Newcomer & Dean (102)]. Subsequently it was shown that other chlorinated hydrocarbon insecticides

such as aldrin, dieldrin, chlordane, heptachlor, and lindane cause similar increased populations of mites even from soil applications [Klostermeyer (103); Michelbacher *et al.* (104)]. Such outbreaks of mite pests have generally been attributed to the destruction of natural enemies including predaceous mites by the new organic pesticides [Clancy & Pollard (105, 106); Lord (107); Pickett (108)]. On the other hand, additional factors may be involved for Hueck *et al.* (109) found an increase in the fecundity of the European red mite, *Metatetranychus ulmi* (Koch), under the influence of DDT and postulated that this was associated with certain critical dosages of the insecticide. Tew & Groves (110) have recently summarized some observations on mite increases in Europe. Field data have provided clear evidence of (*a*) the toxicity of DDT to typhlodromid mite predators, (*b*) an association between DDT applications and high populations of *M. ulmi* and *Bryobia praetiosa* Koch, and (*c*) somewhat less evidence that modes of formulation may influence (*a*) and (*b*). Field observations previously correlated increases in phytophagous species with control of the entomophagous species. Precise laboratory work now casts doubt on the value of typhlodromid mites as a natural control agency for these phytophagous mites. Since predation by other predators was not observed, the authors feel obliged to consider the possibility of an indirect effect of DDT by some other mechanism or direct stimulation of the mites by the insecticide itself. The different population levels of of the mites observed could reflect different levels of stimulation by deposits of DDT of different magnitude, location, and form. This interesting problem has been recently reviewed by Ripper (111) and obviously additional basic studies on the various factors involved are indicated.

Action of acaricides on parasitic mites and ticks.—The previous discussions have been primarily concerned with the activities of acaricides on phytophagous mites. The action of acaricides on parasitic mites and even more so on ticks has been less completely investigated or at least reported. The usual recommendations for control of parasitic mites and ticks suggest chlorinated hydrocarbon insecticides rather than the specific acaricides [Anonymous (112, 113, 114); Traub *et al.* (115); Therrien *et al.* (116); Baker *et al.* (93)]. However, the low toxicity of the acaricides to warm-blooded animals and favorable activity in comparison with chlorinated hydrocarbon insecticides toward certain mites suggest the possibility of much greater application to the problems of parasitic mites and ticks. However certain other considerations such as residual activity, combination control programs, economic considerations, etc., may decrease the practicality of their usefulness. Gasser & Wyniger (31) have investigated the toxicity of Chlorobenzilate to the harvest mite, *Trombicula autumnalis* Shaw, in the laboratory and in preliminary field trials with promising results. Control of the northern fowl mite, *Bdellonyssus sylvarium* (Canestrini and Fanzago) with Neotran, ovex, and Sulphenone has been reported [Furman (117, 118)]. Roberts & Rogoff (119) tried Neotran and Aramite for the control of swine mange. Neotran destroyed most of the mites, *Sarcoptes scabiei suis* Gerlach, but did not eradicate the infesta-

tion and Aramite failed to provide satisfactory control. Chlorobenzilate and Kelthane reduced populations of the fowl tick, *Argas persicus* (Oken), but were not sufficiently residual to clean up the infestation [Rodriguez & Riehl (33)]. Applications of Neotran to cattle for control of *Dermacentor albipictus* (Packard) were ineffective but results with ovex showed some promise, though lindane and chlordane were superior [Weintraub (120)]. In plot tests Hunter *et al.* (121) found that dieldrin was superior to Sulphenone and Neotran for control of the lone star tick, *Amblyomma americanum* (Linnaeus). In the book on parasitic mites of medical and economic importance by Baker *et al.* (93) recommendations or even suggestions for the use of the specific acaricides in control practices are cited in less than one-third of the species discussed. From these limited results it would appear that the acaricides deserve a more intensive examination in connection with the control of parasitic mites and ticks especially for those problems where toxicological and pharmacological considerations are important.

Acaricidal and fungicidal activity.—The far-reaching interrelationships of biological activity are well demonstrated by the combined acaricidal-fungicidal activity of glyodin and Karathane which have been previously discussed. Ovex has been shown to have considerable fungicidal activity for powdery mildew on melons [Lembright (122)], but no effect on those on apples and raspberries [Sprague (123); Vaughan & Pratt (124)]. 1,2-Bis(*o*-hydroxyphenylthio) ethane and bis(*o*-hydroxyphenylthio) methane have appreciable fungicidal activity but no acaricidal activity. Removal of the hydroxy groups results in a loss of fungicidal activity but the resulting 1,2-bis(phenylthio) ethane and bis(phenylthio) methane have considerable acaricidal activity [Cranham, Higgons & Stevenson (17)]. Many of the compounds reported in the patent literature to possess acaricidal activity are also reported to possess fungicidal activity, for example: aryl and alkyl chlorinated anisoles [Barber & Green (125)] and alkyl substituted oxazolines [Davies, Marks & Snow (126)]. Some of these compounds are reported to possess bactericidal or antihelmintic action as well.

Some of the commercial pesticides which are normally considered only as fungicides have demonstrated considerable acaricidal activity. Stoddard, Gries & Plumb (127) obtained excellent control of *T. telarius* in greenhouse experiments with nabam. However, Rich (128) was unable to demonstrate any control of *T. telarius* with nabam or zineb but applications of barium ethylene bis-dithiocarbamate and maneb as well as glyodin and Karathane completely killed both adults and nymphs. Zineb has been shown to inhibit the development of *Tetranychus hicoriae* McGregor on pecans [King & Rosberg (129)]. On the other hand, thiram and captan applications to apple trees in Tasmania increased the populations of *M. ulmi* as has been similarly demonstrated for certain insecticides [Miller (130)]. Filtrates of antibiotic cultures of the *Streptomyces-albus* group applied on apple trees for control of powdery mildew also showed considerable acaricidal effect [Kohler & Fritzsche (131)].

ACTION OF ACARICIDES

Virtually nothing is known of the primary mode of action of the specific acaricides and the systems which they effect. Nor is it known whether or not the lack of or low toxicity of these compounds to insects is due to modification or even absence of such systems in insects or to secondary factors such as detoxication, excretion, transport barriers, etc. Nevertheless there are many important facets of the action of acaricides about which there is considerable information.

Toxicity to different stages.—One of the most characteristic properties of the specific acaricides is the variation in susceptibility of the different stages of mites (egg, developmental stages, adult) to different groups of acaricides. Ebeling & Pence (132) determined the LD_{50}'s of a large number of acaricides to the stages of the two-spotted spider mite, *T. telarius*. The acaricides studied fell into four major groups as follows: (*a*) susceptibility of adult stage > larval stage > egg stage (Aramite); (*b*) adult = larval > egg (Chlorobenzilate, Dimite, and Sulphenone); (*c*) larval > adult > egg (Karathane); and (*d*) larval > egg > adult (Genite, Neotran, and ovex). Meltzer (133) also examined the activities of a large number of acaricides on the various stages of *T. telarius*. The results of Meltzer's studies may be reported in terms of the same four groups as above: (*a*) Sulphenone; (*b*) none; (*c*) Karathane; and (*d*) Chlorbenside, Chlorobenzilate, *p*-chlorophenyl benzene sulfonate, Dimite, diphenyl sulfone, ovex, and Tedion. In general there is very good agreement between the two studies though Meltzer found Chlorobenzilate and Dimite to be comparatively less active to the adult stage than did Ebeling & Pence. This may readily be explained in terms of experimental design.

From these studies the relatively high susceptibility of the larval stage to the specific acaricides is most striking. Even those acaricides such as Chlorbenside, *p*-chlorophenyl benzene sulfonate, ovex, and Tedion, which are primarily considered as ovicides, are actually more effective against the larval stage than the egg stage. All of the acaricides except Karathane show a relatively uniform toxicity to the egg stage. The principal difference lies in toxicity to the adult stage with Aramite, Chlorobenzilate, and Dimite being relatively active against the adults and Chlorbenside, *p*-chlorophenyl benzene sulfonate, ovex, and Tedion being almost inactive. Karathane is unique in showing activity principally against the larval stage.

Ovicidal action.—Hopp (134) in a basic study of the ovicidal action of Chlorobenzilate, *p*-chlorophenyl benzene sulfonate, and ovex found that all three are true ovicides, being able to penetrate the egg shell and kill the embryo. Chlorobenzilate was found to kill the embryo at an earlier stage than the other compounds. Since all three compounds were equally toxic to embryos removed from the egg shell, this difference was attributed to speed of penetration through the shell, the inner layer being the most resistant to penetration. A direct relationship between ovicidal activity and age of the embryo was found, the young embryo being more sensitive than the old.

Normal concentrations of the acaricides penetrated the shell of the winter egg too slowly and insufficiently to be effective due to the penetration-retarding inner wax membrane. Larger doses were effective but caused phytotoxicity.

Types of action.—Blauvelt & Hathaway (135) first reported that eggs of *T. telarius* are killed on the lower surface of the leaf from applications of ovex to the upper surface. This was substantiated for *p*-chlorophenyl benzene sulfonate and ovex on summer eggs of *M. ulmi* by Kirby & McKinlay (136). Cranham, Higgons & Stevenson (17) reported a similar effect for Chlorbenside but not for its sulfoxide and sulfone. Hey (137) has also shown that diphenyl sulfone lacks this property. This effect can also be shown for adult mites with such acaricides as Aramite, Chlorobenzilate, Dimite, Sulphenone, etc., and the residual acaricide responsible for this activity has been designated subcuticular residue as distinguished from surface residue [Ebeling & Pence (138)]. Higher dosage rates are required for control solely by penetration [Cranham, Higgons & Stevenson (17); Ebeling & Pence (132)]. Age and condition of the leaf and species of plant materially affect the activity and effectiveness of subcuticular residues [Ebeling & Pence (132, 138)]. This effect on adults and larvae is apparently due to action as a stomach poison but the ovicidal effect may be due to action in the vapor phase. *p*-Chlorophenyl benzene sulfonate and ovex have been shown to have vapor phase toxicity which was lacking for Chlorobenzilate. The first two compounds show residual ovicidal activity which Chlorobenzilate does not. Chlorobenzilate makes up for this lack of residual ovicidal activity by residual action on the larvae apparently from subcuticular residues [Schäfer (139); Hopp (134)]. An additional type of ovicidal effect has been demonstrated with *p*-chlorophenyl benzene sulfonate and Tedion. The compounds cause sterility of the adult females, eggs laid after contact with residues no longer being viable [Schäfer (139); Huisman, van der Veen & Meltzer (73)].

Residual activity.—Differences in residual field control are basically related to differential intrinsic toxicities and to length of residual activity. The general properties of deposits and residues have been discussed by Gunther & Blinn (4) and the residual activity of various compounds may be compared from half-life values which may be defined as the time required for half of a given quantity of material to react (or dissipate). Half-life values on citrus fruits have been determined for Aramite, 7 to 8 days; ovex, 10; Sulphenone, 9 to 12; Chlorobenzilate, 60 to 80; and Kelthane, 120 to 350 [Gunther & Blinn (4); Gunther & Jeppson (140); Gunther, Jeppson & Wacker (141); Gunther *et al.* (142)] and on pears for Chlorbenside, 11 days, and its sulfone, 7 days [Gunther, Blinn & Barnes (23)]. The relatively long residual activity of Chlorobenzilate on citrus fruits is not commensurate with the relatively poor residual field control obtained for the citrus red mite, *M. citri*. However, relatively high surface residues of Chlorobenzilate are required to kill citrus red mite and thus its ineffectiveness is due to a lower toxicity to this species [Gunther, Jeppson & Wacker (141); Jeppson, Jesser & Complin (30)].

Resistance.—Following the development of resistance by mites to certain of the organophosphorus insecticides [Smith & Fulton (143, 144); Garman (145); Lienk, Dean & Chapman (146); Newcomer & Dean (147, 148)] effective control of resistant strains was obtained with the specific acaricides. Subsequently resistance appeared to many of these compounds with continued use. Mite resistance has recently been reviewed by Smith (149). Although there is a definite lack of published basic laboratory studies on this problem, especially in relation to the specific acaricides, there are a number of references related to observations on control failures. Mite resistance has been reported to azobenzene and Aramite [Pritchard (150)], Aramite and Chlorobenzilate [Jefferson & Morishita (151)], Kelthane, ovex, Aramite, Chlorobenzilate, Chlorbenside, and Tedion [Smith (149)], and ovex [Jeppson *et al.* (62)]. It is very apparent from all reports that resistance problems with phytophagous mites are most serious and are continuing to increase, both as to the number of acaricides and of species of mites involved, not only in the greenhouse but in the orchard and field as well. As yet no basic studies have been reported on the underlying mechanisms of resistance in mites to either the organophosphorus compounds or the specific acaricides nor have any promising leads been reported in relation to basic solutions to this problem.

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ORGANIC PHOSPHORUS INSECTICIDES FOR CONTROL OF FIELD CROP INSECTS[1]

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To give a balanced picture, this review should cover the most destructive pests of the major crops grown throughout the world, since it could not aim at being comprehensive. It should show where the organic phosphorus compounds are effective, where they fail and how they compare with the other available insecticides. Unfortunately this is not possible, if only because many of the necessary investigations have not been carried out—or have not been reported. This viewpoint has, however, determined which papers were selected from the voluminous literature. Where many important papers cover the same topic an arbitrary selection has been made, but less detailed work is referred to where it concerns an important crop or a pest not otherwise mentioned.

Investigations in which organic phosphorus compounds failed to control pests are included but, for the sake of brevity, the dosages used are usually given only when they were effective. There are several notable omissions: the subject of aphid control on potatoes and sugar beet, where the chief concern is to prevent the transmission of virus disease, is omitted because of the recent comprehensive review of the subject by Broadbent (25). Certain pests of leguminous crops are not included because they are discussed elsewhere in this volume (Gyrisco, page 421). Finally the results of investigations on many crops, pests, newer but little tried insecticides, and residues have all had to be omitted for the sake of brevity.

General Pests of Field Crops

There are a few groups of pests which attack a very wide range of crops including many field crops. These will be considered first.

Locustidae.—Many species of grasshoppers and locusts cause incalculable damage to plants of all types throughout the world. The advent of the chlorinated hydrocarbon insecticides has revolutionized control.

As a result of tests carried out in the United States it is agreed that parathion is highly toxic to grasshoppers [Weinman & Decker (170); Gaines & Dean (74)]. The early instars are the most susceptible [Gaines & Dean (71, 74)]. Parathion is also rapid in action but is less persistent than the best chlorinated hydrocarbon insecticides [Brett & Rhoades (23); Gyrisco & Marshall (87)]. Under most circumstances this serious disadvantage, together with its high toxicity, limits the use of parathion though it could be useful on a fodder crop near the time of harvest. It has also been observed

[1] The survey of literature pertaining to this review was completed in April, 1957.

in Oklahoma that a 1 per cent dust was much less efficient at lower temperatures (23). In New York a 1 per cent dust at 60 lb./acre on alfalfa and in Texas a 2 per cent dust at 10 lb./acre on cotton gave excellent control [Gyrisco & Marshall (86); Gaines & Dean (71)]. In Turkey the solitary phase of *Locusta migratoria* (Linnaeus) does extensive damage to rice. Parathion sprays and dusts gave excellent control of nymphs hatched in rice fields of the previous year [Erkiliç & Teoman (62)].

Elateridae.—The many genera of wireworms distributed throughout most of the world attack a great variety of plants. They eat the seeds in the soil or cut and bore into the plants underground. Cultural control techniques are vital on field crops, and in some instances insecticides are economically justified. Chlorinated hydrocarbon types are usually employed.

Parathion has been extensively tested against wireworms and, although it sometimes fails to give control, it has usually proved fairly effective. It is less persistent than most of the chlorinated hydrocarbon compounds and, while this is usually a disadvantage, there are circumstances where it may be advantageous because toxic residues are avoided. Application may be to the seed, or to the furrow as the seeds are sown, or by disking into the soil some time before planting.

Fairly good protection of maize against *Melanotus communis* (Gyllenhal), the corn wireworm, has been obtained by seed dressing without reducing the germination, but this method was less effective than drilling in with the seed, and parathion was less effective than dieldrin, heptachlor, aldrin, and lindane [Dogger & Lilley (48); Kulash & Monroe (106, 107)].

Potatoes were also well protected by cultivating parathion at 4 lb./acre into the soil before planting [Merrill (123)]. Doubtless because of its volatility it has been found less satisfactory at higher soil temperatures [Kulash (105)]. Demeton and EPN have both proved inferior to the chlorinated hydrocarbon insecticides [Kulash & Monroe (107)]. Diazinon was also comparatively ineffective [Starks & Lilly (155)]. Against *Limonius* spp. in California parathion was inferior to lindane [Lange, Carlson & Leach (109); Lanchester (108)] and when applied to the soil in row treatments at 1 or 2 lb./acre in Alabama it did not protect sweet potatoes against the important pest *Conoderus amplicollis* (Gyllenhal), the gulf wireworm [Griffin & Eden (82)]. In France, dusting the seed balls of beet and the seeds of wheat, barley, oats and maize with parathion preparations did not materially affect germination and increased yields up to 39 per cent. Parathion also controlled the adult of the wireworm concerned, *Agriotes obscurus* (Linnaeus) [Bonnemaison (19)]. Where soil residues of more persistent insecticides are to be avoided 4 lb./acre EPN immediately cultivated in can give good control of *Agriotes mancus* (Say), the wheat wireworm [Merrill (123)]

Pseudaletia unipuncta (Haworth).—The armyworm occurs in many parts of the world and attacks corn and other Gramineae and some Leguminosae. The larvae feed at night and spend the day in the soil. When a crop has been devoured, they move in droves to new fields. Toxic baits are often

used to poison the larvae and dusts of 10 per cent DDT or 2 per cent BHC are also effective.

In laboratory tests parathion was more toxic at the LD_{50} level than eight other organic insecticides including DDT, aldrin, dieldrin, chlordane, and toxaphene. It also gave the fastest kill. But the $L_{50}D/LD_{99}$ ratio was not the lowest, suggesting that toxaphene or dieldrin might be more effective in practice [Weinman & Decker (171)]. In tests in Ohio, parathion at 0.05 per cent was also more toxic than various dosages of chlorinated hydrocarbon insecticides when the larvae were caged with sprayed plants. The parathion acted rapidly and there was almost no feeding [Hibbs & Weaver (93)]. A field test in New Jersey with 1 per cent parathion dust killed only younger larvae and was inferior to baits [Filmer & Ginsburg (67)].

Laphygma frugiperda (J. E. Smith).—The fall armyworm is commonly found in the tropical and subtropical regions of North and South America. The larvae probably prefer the foliage of maize and other cereals but they attack many other plants. Natural enemies often give good control but, where they fail, insecticidal methods used against the army worm are efffective.

In Virginia 0.5 per cent parathion dust was as effective as 3 per cent DDT and it killed larvae deep in the buds and whorls of maize more consistently. But DDT was preferred on grounds of performance, cost, and toxicity to operators. The treatments are likely to destroy the parasites and predators [Hofmaster & Greenwood (95)]. In Mexico and Colombia, where the fall armyworm is one of the principal pests of maize, parathion sprays gave complete control but were less lasting than various chlorinated hydrocarbon insecticides. A 1 per cent dust was also highly effective and lasted well for twenty days [Leiderman (111); Ruppel, Benavides & Saldarriaga (144)]. Parathion also prevents the eggs hatching [Fenjves (63)]. *Laphygma exempta* (Walker), the African armyworm, was also readily controlled by 0.02 per cent (approximate) parathion spray [Whellan (175)].

Cutworms damage a great variety of plants and are of world-wide distribution. Where natural enemies and cultural techniques fail to give control, chlorinated hydrocarbon insecticides may be applied in bands along the crop rows. Baits and certain dips applied to seedlings at the time of transplanting are also effective.

Agrotis segetum (Schiffermüller), attacks beet, lucerne, and maize in Northern Italy and is a serious pest in other parts of Europe. Parathion at 0.36 lb./acre as a spray gave complete control and was better and cheaper than the DDT or BHC treatments also tried. It was, however, more costly than baits [Rota (143)]. *Agrotis ypsilon* (Rottemburg), the black cutworm, attacking vetch grown for seed was very poorly controlled by malathion at 0.5 lb./acre, and toxaphene plus DDT was much superior [Randolph (137)].

Wheat and Other Small Grains

There are many important insect pests of the small grains some of which are of almost world-wide occurrence, for example, *Phytophaga destructor*

(Say), the hessian fly; *Cephus* spp., the wheat stem sawflies; *Oscinella frit* (Linnaeus), the frit fly, but control of these insect pests depends, for practical and economic reasons, on cultural techniques. However, there are certain exceptions. For example, BHC has given good results as a seed dressing against wireworms, notably in the Western United States and Canada, and parathion has been used against the greenbug and tested against the chinch bug.

Toxoptera graminum (Rondani).—This aphid, sometimes called the greenbug, feeds on a variety of Gramineae but is most troublesome on wheat and oats. It is widely distributed and estimated to cause a loss of 1 to 3 per cent of the wheat crop throughout the world. At certain times it causes enormous losses, for example, 21.8 per cent of wheat crop in Oklahoma [Fenton & Dahms (64)].

Control normally depends on cultural practices such as clearing away volunteer grain in the spring or on natural enemies, but when these failed or were neglected, parathion was dramatically successful. In the Oklahoma outbreak grain worth $3,923,616 net was saved [Fenton & Dahms (64)]. Parathion has been applied by low volume sprayers, mist blowers, from aircraft, and by power dusters. At about 0.25 lb./acre the control was 93 to 100 per cent in seven days. Parathion was more effective than BHC or TEPP The temperature at the time of treatment and for three hours afterwards should be at least 50° F. for parathion. As an alternative Metacide or TEPP may be used. For the latter, the temperature should be 75° F. or above. [Dahms (37, 38)]. It can be assumed that, if the need arose, essentially the same treatment would be effective against other aphids on small grains.

Blissus leucopterus (Say).—Besides attacking corn, the chinch bug is an important pest of wheat and other small grains. On wheat an application of 0.5 lb./acre of parathion gave a high initial kill but was of no value two to three days later, whereas endrin was still very effective [Gannon & Decker (78)].

Eurygaster integriceps Puton.—This pentatomid is a serious pest of wheat in Syria and Turkey. The older stages are more resistant, and it is best to apply insecticides when the earlier instars are present. Parathion 0.75 per cent dust applied under a drag sheet, aircraft applications of parathion at 0.35 lb./acre, and Diazinon at about 0.6 lb./acre from emulsion concentrates have all given excellent control [Talhouk (159, 160); Nizamlioglu (125)].

Maize or Corn

Maize is extensively grown in the United States (which produces about 60 per cent of the world crop), in the Danube river basin, and in Russia, India, Mexico, Argentine, Brazil, South Africa, and Egypt. In the United States it is the most important field crop, and it is estimated that about 9 per cent is destroyed annually by insects. It is not usual, for economic rea-

sons, to apply insecticides to field corn, but sweet corn is frequently treated.

Heliothis zea (Boddie) and *Heliothis armigera* (Hübner).—These corn earworms are probably the most important pests of corn in the New and Old Worlds respectively. Control on field corn depends on cultural practices and natural enemies, of which several are important, but on sweet corn DDT emulsions are employed.

Parathion dusts and sprays give poor control compared with DDT when applied to the ears and, naturally, therefore more general applications are ineffective [Kulash (104); Rutschky (145)]. In Texas, with high day temperatures, 1 per cent parthion dust blown into the leaf whorls at weekly intervals gave good control, and sprays were also effective [Wene & Blanchard (173)]. This latter result must be regarded as exceptional and was probably due to a fumigant action at the high prevailing temperature.

TEPP is not effective [Ivy & Ewing (98)] and schradan is inactive at high dosages [Ivy, Iglinsky & Rainwater (99)]. Malathion is inferior to DDT [Hayslip *et al.* (92); Ditman, Todd & Harrison (47)], and so is Chlorthion [Fife & Walker (66)].

Pyrausta nubilalis (Hübner).—The European corn borer is a very serious pest of maize in Europe, parts of Asia, and America. Destruction of crop residues and various other cultural techniques are fundamental for control. There are important parasites and predators. The larvae, after feeding between the leaves, bore into the stalk and ears and continue to feed there. Control measures are practiced chiefly on sweet corn. Control is by DDT applied when the eggs begin to hatch but, if residues on fodder must be avoided, rotenone or ryania can be used.

Parathion gives good control and can also be used where the plants are to be used for forage. In Illinois 2 per cent parathion dust from aircraft gave control of second generation borers superior to that of 5 per cent DDT dust on sweet corn. The residue in silage was negligible [Apple & Decker (11)]. When parathion in oil was applied to the ears, it was superior to DDT in oil [Apple & Decker (12)]. Despite these favourable results, ryania and DDT are considered more practical [Hawkins & Thurston (91)].

In Italy the European corn borer is usually controlled by natural enemies, but it has increased in recent years due to the introduction of susceptible varieties from the United States and the growing of second crop maize. Parathion sprays have given satisfactory control. But to avoid destroying the natural enemies it should only be used against the second generation. In any case, chopping the stems to destroy the larvae before using for animal bedding is much cheaper [Baldoni (14); Grandori & Rota (81)].

In Germany, in September, when the larvae were in the lower third of the plants parathion, methyl parathion, Potasan, and demeton were ineffective. But the exposed larvae were killed by parathion emulsion, by methyl parathion dust, and by BHC plus DDT. The latter combination was recommended [Fickewirth (65)].

In Iowa, EPN sprays and granulated formulations at 0.5–0.6 lb./acre have given control equal to DDT. There was no damage to the plants. Malathion was inferior at about twice the dosage [Questel & Brindley (134); Cox *et al.* (33)]. The rate of loss or deterioration of malathion in deposits was apparently too rapid for it to give satisfactory control [Cox, Fahey & Brindley (34)].

Blissus leucopterus (Say).—The chinch bug attacks Gramineae in the southern part of Canada, the United States, Mexico, and Central America. In parts of America it causes enormous losses. Adults and nymphs suck the sap from the stems of the host plants.

Control is by various cultural practices and the construction of barriers to stop or kill the walking bugs, or by applying chlorinated hydrocarbon insecticides around the edge of the crop, if the bugs are concentrated there. In Illinois, where the bug is a particularly serious pest, it was found that small doses of parathion applied to the soil killed all bugs caged on it for 24 hr. even 13 days after the soil had been treated. Endrin was, however, the preferred insecticide for barriers [Gannon & Decker (77, 78)]. As a margin spray, parathion at 0.5 lb./acre killed bugs present at the time of spraying. It was more toxic than lindane, dieldrin, endrin, or aldrin, but only dieldrin and endrin had sufficient residual action to prevent reinvasion for more than two to four days [Decker, Bigger & Weinman (45)].

Lucerne and Clover

A separate review will be found in this volume which covers many pests of forage crops in the United States (Gyrisco, p. 421). Here insects which are chiefly important on crops of lucerne and clover grown for seed, or which occur in other parts of the world, are discussed.

Lucerne or alfalfa (*Medicago sativa* and other spp.) is very widely grown and in the United States it is the most important forage crop. Clovers, *Trifolium* spp., and sweet clovers (*Melilotus* spp.) are also grown on large areas in many parts of the world.

Adelphocoris lineolatus (Goeze), the alfalfa plant bug; *A. rapidus* (Say), the rapid plant bug; *Lygus lineolaris* (Palisot de Beauvois), the tarnished plant bug; and also *L. hesperus* (Knight) are destructive pests on lucerne grown for seed. A single spray of 0.5 lb./acre parathion gave good control of these bugs at the same time as *Empoasca fabae* (Harris), the potato leafhopper [Wilson (179)]. A 1 per cent parathion dust applied by helicopter gave a high kill but, owing to the rapid growth of the plants, protection was not satisfactory at the end of two weeks [Gyrisco & Marshall (86)]. A spray giving 0.33 lb./acre parathion controlled *A. lineolatus* but where residues are not objectionable DDT or aldrin are superior and safer to apply [Medler (122)]. TEPP was highly toxic to *L. lineolaris* but not persistent while schradan was ineffective [Zia-ud-Din (184)].

Sminthurus viridis (Linnaeus), the lucerne flea, is an important pest in Australia. It was well controlled by parathion but individuals hatching

from eggs present at the time of treatment were not killed [Wallace (167)]. Malathion was effective at 1 oz. 50 per cent malathion miscible oil per acre [Doolette (52)]. In Tasmania excellent results were obtained with 1 oz./acre actual malathion or 0.5 oz./acre parathion (8).

Phytodecta fornicata (Brüggemann).—Parathion as a 1 per cent dust or at 0.06 per cent as an emulsion spray gave a high kill of this leaf beetle which attacks lucerne in Serbia and Macedonia but it was less persistent against the general insect population than DDT [Tanasijević (161)].

Apion aestivum (Germar), syn. *A. trifolii* (Linnaeus), and other clover seed weevils damage clovers in Europe. In Switzerland a parathion spray applied during the week before flowering began, considerably increased the seed yields [Schenker (148)]. Adults of *Hypera brunneipennis* (Boheman), the Egyptian alfalfa beetle, were not controlled by EPN applied to the stubble to kill them before oviposition could take place. But at 0.25 lb./acre as a spray EPN and methyl parathion both gave promising results against the larvae and were superior to parathion and malathion [Reynolds, Anderson & Deal (138)].

In a comparison of various phosphorus insecticides against *Hypera meles* (Fabricius), the clover head weevil and *Hypera nigrirostris* (Fabricius), the lesser clover leaf weevil, on crimson clover in Georgia Thimet at 1.0 lb./acre as a spray gave better control, as assessed by counting the larvae remaining on the plants, than parathion, malathion or Chlorthion [Beckham (16)]. Against *Hypera punctata* (Fabricius), the clover leaf weevil, on mixed red clover and alfalfa four applications of 0.25 lb./acre parathion gave very poor control [Bigger & White (17)].

Sitona cylindricollis (Fahraeus), the sweet clover weevil, attacks the crop in the United States and Canada. Dusts or sprays of 1.0 lb./acre parathion gave good control in Indiana though DDT may be preferred because it is less dangerous. EPN at 1.0 lb./acre was inferior to parathion. Comparative tests show that parathion is one of the most toxic compounds to this insect, but it gave less effective protection in the field tests in Canada than dieldrin and heptachlor when compared at 0.5 lb./acre [Allen & Kelleher (4); Allen & Askew (3); Wilson (180)].

Tychius stephensi (Schönherr), the clover head weevil, was well controlled by a dust giving 0.5 to 1.0 lb./acre parathion [Gyrisco & Marshall (86, 87)]. In Canada *Miccotrogus picirostris* (Fabricius), which is thought to be responsible for the reduction in a seed yields of alsike clover, was controlled by dusts and sprays at dosages of 0.5–2.0 lb./acre parathion [Pielou (133)]. To obtain practical control of the clover root borer, *Hylastinus obscurus* (Marsham), at least 0.75 lb. per acre of parathion was required, and γ BHC was more effective [Gyrisco & Marshall (85)].

Beans and Peas

Beans, *Phaseolus* spp. and *Vicia* spp., and peas, *Pisum sativum*, are grown in many parts of the world and are attacked by a variety of insects.

Aphis fabae Scopoli.—The black bean aphid is widely distributed but is chiefly important as a pest of *Vicia* in Europe. In Germany it has been found that, provided the temperature is about 24° C., parathion at 0.008 to 0.02 per cent will give complete kills but at lower temperatures (10° C.) it is less effective [Dosse (54)]. Incomplete kills are to be avoided since parathion destroys many natural enemies and the aphid population may recover very quickly. The protection is also not very long lasting [Way, Smith & Potter (169)]. It is approved for use in Great Britain at 0.05 to 0.1 per cent (10). On Lima beans, in New York, four applications of parathion or TEPP applied against *Tetranychus telarius* (Linnaeus), the two spotted spider mite, gave good control of *A. fabae* [Hackett (88)]. In Britain 0.025 to 0.06 per cent sprays are approved for immediate control (10).

The systemic insecticides schradan and demeton are both effective against *A. fabae* and certain other aphids whether applied to the seed, watered on to the soil, or sprayed over the plants [David & Gardiner (39, 40, 42); Jancke (103); Lhoste & Leibovici (114); Unterstenhöfer (163); Chaudhary (32)]. In practice in Britain applications are made by spraying the crop with 0.07 to 0.20 per cent sprays (10). Demeton 0.05 per cent spray, applied to spring sown broad beans soon after the primary migration into the crop had ceased, also gave good control and some residual toxicity for five days and was superior to DDT. Treatments produce large increases in yields when the aphid infestation is heavy but the economics are uncertain since a threatened attack may not develop. Demeton and parathion are toxic to coccinellid predators [Way *et al.* (169)]. Malathion as an 0.057 per cent spray is also approved in Britain for controlling the black bean aphid (10).

It may be concluded that TEPP and parathion are cheaper but give less lasting protection than the more costly schradan, demeton, or methyl demeton. The difference in price is therefore to an extent cancelled, especially when the damage to the crop caused by repeated application is considered. A good insecticide applied at the end of the primary migration into the bean crop combined with early sowing can give a striking increase in yield [Hunt (97)].

Macrosiphum pisi (Harris).—The pea aphid is a widespread pest of peas. Control in the United States is discussed in the article by Gyrisco to which we have already referred. In general it has been found that the organic phosphorus compounds, especially those which are more lasting, give good control. In Sweden plants grown from peas soaked in dilute schradan solutions gave almost complete kills of the aphid when infested one month after sowing [Andersson & Ossiannilsson (5)]. In Britain schradan at 14.5 oz./acre, demeton at 16 oz./acre, and DDT at 100 oz./acre all gave outstanding control. DDT and demeton also gave outstanding control of thrips; of the three, DDT is considered the best choice. Malathion at 12.8 oz./acre and parathion at 8 oz./acre gave inferior control (6). It may be added that DDT also has the advantage of giving good control of the pea moth, *Laspeyresia nigricana* (Stephens).

Epilachna varivestris Mulsant.—The Mexican bean beetle is a serious pest of beans. Both the larvae and adults feed on the undersides of the leaves.

TEPP has given good control on Lima beans on Long Island and it is accepted for use in Canada in sprays at about 0.02 per cent. As it is not persistent, repeated applications may be required [Hackett (88); Martin (121)]. Four applications of parathion at 0.1 lb./acre as a dust controlled the larvae and significantly increased the yield of snap beans in Virginia [Brannon (21)]. Two applications of a 1 per cent dust were effective in Mexico [Enkerlin (61)]. Rotenone gives good control and, because of its safety, it is to be recommended. When parathion is applied a 0.05 per cent spray or a 2 per cent dust may be used, but not within 15 to 21 days of harvest, according to the crop. Malathion is also effective at 0.1 per cent spray or as a 5 per cent dust and can be used within three days of harvest (7). When compared with malathion, Dilan has been found superior though, unlike malathion, it was not effective against aphids and mites present on snap beans [Ditman, Rosenberger & Harrison (46)]. EPN has given poor control [Brett & Brubacker (22)].

Bruchus rufimanus Boheman.—This bean weevil attacks broad beans in many parts of the world. Parathion at 0.36 lb./acre sprayed as soon as the lower flowers began to wither gave good control if the weather was warm enough (above 17° C.) for the beetles to be active. DDT was also effective [Franssen (69)].

Bruchus pisorum (Linnaeus).—To obtain effective control of the pea weevil it is necessary to maintain a good coverage with the insecticide during the oviposition period. Parathion applied three times as a spray or as a dust was very effective as assessed by the population and damage to the pods. A 1 per cent dust was equal to 5 per cent DDT. Malathion spray also gave a good control, but a 2.5 per cent dust was inferior to 2.5 per cent DDT [Davis & Swenson (43); Schopp, Brindley & Hinman (149)].

Apion godmani Wagner.—Repeated applications of a 1 per cent parathion dust or a 0.05 per cent spray begun when the beans were in flower were effective against this weevil attacking beans in Mexico [McKelvey *et al.* (120)]. There would be a considerable danger of destroying pollinating insects unless the applications were properly timed.

Nezara viridula (Linnaeus).—The green vegetable-bug sometimes causes total loss of bean crops in New Zealand. It may be controlled by spraying with 0.0125 to 0.025 per cent TEPP [Brien *et al.* (24)].

Phytomyza atricornis Meigen.—This and other leaf miners, *Liriomyza* spp., sometimes damage peas in Britain and appreciably reduce the yield. Parathion 0.05 per cent spray gave good control of the larvae within the leaves, whereas DDT was only effective against the adult flies and young exposed larvae [Dunn & Wright (57)]. This result is in general agreement with those obtained with allied species on other crops in the United States [Wilcox & Howland (177)].

Cruciferous Crops

Cabbage, Brussels sprouts, kale, turnips, swedes, etc. are grown in many parts of the world for direct consumption or as seed crops. All parts of the plants are attacked by insects but only some of the most important pests can be considered.

Erioischia brassicae Bouché.—The cabbage maggot or the cabbage root fly is a widely distributed pest in Europe and North America. As the name indicates, the larvae feed on the roots of cruciferous crops. Calomel (mercurous chloride) was used for control, but this has been replaced by the chlorinated hydrocarbon insecticides. Under most circumstances parathion was effective. When used as a dip for the roots and stems just before planting out it gave excellent protection for up to three months [Eide & Stitt (58); Endrigkeit (59)]. It was also effective when watered on to the base of the plant [Wright (181)]. In Germany applications made to tne plant bed three to four weeks before infestation began gave excellent protection [Endrigkeit (60)]. Malathion was ineffective when placed in the furrows with turnip seeds [Stitt (156)].

Psylliodes chrysocephala Linnaeus.—The larvae of the cabbage stem flea beetle damage cabbage in the autumn and winter by boring in the stems and leaf petioles. In Holland, where it may be a limiting factor in rape growing, parathion was less effective than DDT against the adults. However, parathion killed the larvae in the leaf stalks whereas demeton and schradan had little effect [Veenenbos (165)].

Brevicoryne brassicae (Linnaeus), *Rhopalosiphum pseudobrassicae* (Davis), and *Myzus persicae* (Sulzer).—The cabbage, turnip, green peach and other aphids may be found on various Cruciferae and in some districts an seasons may destroy or reduce the value of the crops. In a general way it can be expected that organic phosphorus insecticides will give at least good temporary control of these aphids. The literature is extensive and it is only possible to mention the most important points. TEPP was effective against all three species as dusts and sprays. The effectiveness of the dust was greatly decreased at lower temperatures, by moisture on the foliage, or by wind. TEPP does not, of course, give lasting protection and aphids concealed within the plants are not killed. This is a disadvantage for aphid control but permits it to be used just before the crop is harvested. Parathion was also generally effective and more persistent than TEPP and less affected by a drop in temperature [Bronson & Stone (26); Wene & White (174); Walton & Howell (168); Fjelddalen (68); Jacks & Lamb (102)]. Furthermore, when applied to one surface of a leaf parathion can penetrate and kill aphids on the other surface. It can also act as a fumigant but it has the disadvantage that it kills a wide range of aphid parasites and predators and as a result a very rapid build-up of the pest population may occur later [Ripper, Greenslade & Hartley (141)]. The compounds which are truly systemic are, however, most useful since aphids sheltering within a crucif-

erous plant, well away from any leaf on which the spray falls, are killed and because they are persistent [Wright & Wheatley (182)]. Such compounds can also be applied to the roots and to the seeds [Chaudhary (32)]. One of the first to be developed was schradan; this had the outstanding and almost unique advantage of low contact toxicity, so that the effects of residues on natural enemies, e.g., *Aphidius brassicae* (Marsh), *Coccinella septempunctata* (Linnaeus), and syrphid larvae were not great and they survived and prevented a rise in populations [Ripper *et al.* (140, 141)]. It is approved for use in Great Britain on Brussels sprouts at 0.02 per cent (10). Demeton is also effective [Dowdy & Sleesman (55); Reynolds, Anderson & Swift (139); van Hoof (164)]. Because of its contact toxicity it acts more rapidly than schradan but is also often destructive of the natural enemies. Methyl demeton, which is less toxic to handle, has given good control of *B. brassicae* on Brussels sprouts lasting twelve days [Austin & Linke (13)]. The losses caused to sprouts by *B. brassicae* and the economic return to be expected from applying systemic insecticides have been investigated in Britain. It is concluded that aphid control on the maturing plants in August and September may be worthwhile, but that a greater general increase in yield could be obtained by keeping the newly transplanted sprouts aphid-free so that they made good growth. It might be possible to do this at nominal cost by applying the systemic insecticide to the plants in the seed bed [Strickland (157)].

Murgantia histrionica (Hahn).—The harlequin bug is usually controlled by DDT, toxaphene or rotenone. In laboratory tests parathion was more toxic than BHC or DDT [Gaines & Dean (73)].

Eurydema ventralis (Kolenati).—In France it has been found that heavy infestations of this pentatomid sometimes kill young *Brassica* plants. Parathion at about 0.02 per cent as a spray or as a 1 per cent dust gave a high kill [Bonnemaison (19)].

Pieris spp.—The cabbage white butterflies are widely distributed and, in some seasons, serious pests of *Brassica* crops. Natural enemies give an important measure of control. DDT and some of the older insecticides are usually recommended but parathion and malathion have also been effective in Wisconsin [McEwen & Chapman (117)]. Schradan and demeton are comparatively ineffective [Ripper, Greenslade & Hartley (140); Ripper, Greenslade & Lickerish (142); David & Gardiner (41)].

Trichoplusia ni (Hübner).—Larvae of the cabbage looper also damage cruciferous crops. Three to five applications of a 2 per cent parathion dust alone or with DDT gave good control in southern California. Malathion 5 per cent dust and diazinon 4 per cent dust were inferior [Wilcox & Howland (176)]. In Texas 5 to 7.5 per cent malathion dusts have proved effective and it was also found that malathion could be usefully combined with DDT or rotenone [Wene (172)]. In western New York, where the loopers are very resistant to DDT, a spray giving 1 lb./acre parathion gave poor control when assessed three days later [McEwen & Hervey (118)].

Ceuthorhynchus rapi (Gyllenhal).—In Germany the large cabbage shoot weevil was well controlled by parathion dust or spray applied at five-day intervals [Dosse (53); Buhl (27)].

Ceuthorhynchus assimilis (Paykull).—The cabbage seed weevil often causes serious loss of rape seed directly and also makes possible infestation by *Dasyneura brassicae* (Winnertz), the brassica pod midge. Parathion dust or spray applied as soon as blossoming is complete, to avoid destroying bees, has given good control of both insects in the United States and in Germany [Crowell (36); Holz (96); Godan (80)]. In Holland, where *C. assimilis* together with *Psylliodes chrysocephala* the cabbage stem flea beetle, had become limiting factors in rape growing, parathion applied when the plants were beginning to flower, give disappointing results and was inferior to BHC and dieldrin. It did not kill young *D. brassicae* larvae within the pods and was less effective than DDT against the adult *P. chrysocephala*, but it did kill larvae of the latter in the leaf stalks, whereas demeton and schradan had little effect [Veenenbos (165)]. In Sweden methyl parathion also controlled *C. assimilis* and thereby largely protected spring rape from *D. brassicae* [Sylvén (158)].

Potatoes

Leptinotarsa decemlineata (Say).—The Colorado potato beetle, as explained below, has ceased to be an important pest of potatoes in the United States; but in western Europe, to which it was transported, it is very destructive. The adults and larvae feed on the foliage and may also spread certain fungous diseases. For control, calcium arsenate or lead arsenate were used until DDT was discovered.

Parathion is not considered satisfactory for Colorado-potato-beetle control [Schrader (150)] but it is interesting to note that in the laboratory an 0.1 per cent spray prevented the eggs from hatching [Schwartz (151)]. In field tests in Italy an 0.2 per cent spray killed a high percentage of insects and increased the yield enormously. In the same field tests it was found that a 0.14 per cent schradan spray gave very good control and also increased the yield nearly as much as parathion [Bonetti (18)]. This latter result is surprising and would seem to need confirmation. In Germany 2 per cent Potasan has been found to be very toxic to Colorado potato beetle adults and larvae [Schrader (150)]. In Canada 4 per cent malathion or Diazinon dusts at 30 to 50 lb./acre have been found to give satisfactory control [Martin (121)].

In commercial growing areas in the United States the treatments with DDT which have to be made in most cases for controlling the potato leafhopper, *Empoasca fabae* (Harris), also control the Colorado potato beetle so satisfactorily that it has ceased to be regarded as an important pest.

Empoasca fabae (Harris).—The potato leafhopper is the most serious pest of potatoes in the United States. Many plants besides potatoes are attacked. The insects suck the sap from the veins on the undersides of the

leaves and their feeding causes the symptoms of discolouration and distortion of the leaves known as hopperburn. DDT or sometimes toxaphene are used for control.

In tests on potatoes in Ohio a 0.05 per cent (approximate) parathion spray gave complete control and malathion was effective at the same concentration. Demeton gave complete control at about one and one-half times this concentration and was superior to EPN [Sleesman (154)]. In Canada also 4 per cent malathion dusts and 0.05 per cent sprays and demeton sprays are recognised as being effective [Martin (121)]. Schradan was ineffective [Dowdy & Sleesman (55); Sleesman (154)].

Gnorimoschema operculella (Zeller).—The potato tuberworm is widely distributed in potato growing areas throughout the world. Damage is done by the larvae living on the leaves, stems and tubers. DDT is usually used for control.

Parathion has been applied in Italy against this pest. In field tests 0.008 to 0.0125 per cent parathion sprays killed over 90 per cent of the larvae in the leaves of lightly infested plants but only 3 per cent of the larvae in the tips. At 0.125 per cent DDT spray killed 90 per cent of all larvae [Bartoloni (15)].

Epitrix cucumeris (Harris).—The potato flea beetle adult and larvae injure potatoes seriously. Chlorinated hydrocarbon insecticides give good control. When tested on potato plots in Ohio sprays of 0.04 per cent parathion, 0.5 per cent malathion, or 0.6 per cent (approximate) demeton were all inferior to chlorinated hydrocarbon insecticides [Sleesman (154)]. Four applications of a Diazinon spray giving 1 lb./acre active ingredient at each application gave excellent control, but dieldrin and endrin were somewhat better [Hofmaster (94)]. A 4 per cent Diazinon dust at 30 to 40 lb./acre and an 0.05 per cent spray are recognised for use in Canada [Martin (121)].

Cotton

Cotton is widely grown in the world. The United States produces about 30 to 40 per cent of the total crop and is followed by the U.S.S.R., China, India, Brazil, Egypt, and Pakistan. In the larger producing areas, the standard of cultivation is high. In countries such as Uganda, Nigeria, Tanganyika, and Nyasaland, where it is produced by African farmers, the standard is much lower but it is nevertheless an important cash crop. The cotton plant with its abundant fruit and foliage is attractive to many insects which cause enormous losses. The subject of cotton insects and their control in the United States has been reviewed recently [Gaines (70)].

Anthonomus grandis (Boheman).—The boll weevil causes enormous, though variable, losses in the principal cotton growing areas of the United States amounting to 20 to 40 per cent of the crop. Cultural techniques can give valuable control and these should always be used on economic grounds.

The boll weevil is difficult to control with insecticides because the

adults do not feed on the surface tissues and larvae develop within the squares and bolls. Despite the difficulties, chemical control has been extensively practiced. Calcium arsenate, alone or in combination with nicotine to control aphids, was used until the discovery of the chlorinated hydrocarbon insecticides. These have given good results but in 1954 evidence of resistance was obtained. It is evident that an effective organic phosphorus insecticide would be valuable if further resistant strains developed or if it would control the larvae developing within the squares.

It has been shown that the adults are less resistant to most insecticides in July than in October and this is also true of parathion [Rainwater & Gaines (136)]. In the field, in Georgia and Texas, parathion has not been successful in reducing the number of weevil punctured squares and in further tests it was not effective compared with toxaphene and calcium arsenate [Loden & Lund (115)].

Besides the disappointing results against the adults, parathion dusts and sprays were ineffective against the larvae developing within the squares, whereas chlordane caused a high mortality [Rainwater (135); Gaines & Scales (76); Lukefahr & Gaines (116)]. In laboratory tests methyl parathion has been shown to be more toxic to the boll weevil than parathion [Ivy *et al.* (100)].

TEPP dust was not effective [Ivy & Ewing (98)]. Schradan was ineffective as a seed dressing or as a spray [Ivy, Iglinsky & Rainwater (99)]. Methyl parathion gave satisfactory control of the overwintering brood but it did not kill larve developing within the squares [Fife & Walker (66); Lukefahr & Gaines (116)]. It should be used at 0.25 to 0.5 lb./acre. Malathion is effective at 1.0 to 3.0 lb./acre (9).

EPN dusts have been effective at 2.5 to 3.0 per cent [Rainwater & Gaines (136); Fife & Walker (66)]. In sprays 0.4 to 0.5 lb./acre EPN applied repeatedly have given good control in Louisiana and South Carolina [Young & Gaines (183); Fife & Walker (66)]. It is not however effective against the larvae developing within the squares (116). It is recommended for use at 0.5 to 0.75 lb./acre (9). EPN would have to be mixed with a chlorinated hydrocarbon type of insecticide to produce a comprehensive treatment for cotton pests.

Chlorthion was only satisfactory against the more susceptible overwintering brood [Fife & Walker (66); Pfrimmer & Gaines (131, 132)]. Seed treatments with Thimet gave protection against the overwintering brood for about four weeks after plant emergence. Better results can be obtained with conventional early season sprays [Parencia, Davis & Cowan (128)].

Eutinobothrus brasiliensis (Hambleton).—This weevil and *Aphis gossypii* which were doing the most damage to cotton in Brazil were controlled by 0.5 per cent parathion dust and an increase in yield resulted. At 0.125 per cent in dust and 0.01 per cent in sprays parathion was not effective [Lepage & Gianotti (112, 113)].

Pectinophora gossypiella (Saunders).—The pink boll worm is among the

most serious insect pests in the world and occurs in most cotton growing areas. Control is by quarantine, cultural methods, and DDT.

The pink bollworm does considerable damage to cotton in Sicily reducing the yield 20 to 30 per cent. Four applications of parathion sprays at 0.1 to 0.5 per cent applied from the end of July to the beginning of October significantly reduced the number of infested bolls but the level of control was still unsatisfactory [Petralia (130); Scavone (147)]. It has also been found in Texas that if parathion at 10 lb./acre is sprayed on to infested bolls in the field before they are buried emergence of adults is reduced greatly [Shiller & Chapman (152)]. Methyl parathion used in conjunction with DDT gave good control and held a wide range of cotton pests in check [McGarr (119)]. The only organic phosphorus compound recommended is Guthion at 0.75 to 1.0 lb./acre (9).

Heliothis zea (Boddie).—Second- and third-generation larvae of the bollworm, are important pests on cotton. For control, calcium arsenate has been replaced by such chlorinated hydrocarbons as DDT, BHC, toxaphene, and endrin either alone or in combination.

Guthion at 0.75 to 1.0 lb./acre is recommended for use against the bollworm (9). In contrast, the following organic phosphorus compounds did not give control—parathion 2 per cent [Gaines & Dean (72)]; HETP 5 per cent [Ivy & Ewing (98)]; schradan systemically and as a spray [Ivy, Iglinsky & Rainwater (99)]; Chlorthion [Fife & Walker (66)].

Alabama argillacea (Hübner).—The cotton leafworm is a tropical insect but it migrates into the United States. It is readily controlled by most chlorinated hydrocarbon insecticides except DDT.

Parathion is very effective against the cotton leafworm. Good results were obtained in Brazil [Lepage & Giannotti (112)], Venezuela [Fenjves (63)], and in the United States, where doses ranging from 0.1 to 0.25 lb./acre gave satisfactory control [Ivy & Scales (101); Davis, Cowan & Parencia (44)]. In many experiments it was superior to toxaphene, endrin, and calcium arsenate, and it is among the recommended insecticides [Mistric & Martin (124); see also (9)]. Methyl parathion at 0.25 lb./acre also lasted longer than various chlorinated hydrocarbons and is recommended at 0.125 lb./acre (9, 44, 66). Schradan was quite ineffective [Ivy *et al.* (99, 101)]. Malathion was effective but less persistent than parathion. It should be used at 0.25 to 0.5 lb./acre (9, 44, 101). EPN was effective and lasting at 0.5 lb./acre [Parencia, Cowan & Davis (127)]. It is recommended at 0.25 to 0.5 lb./acre and so is Guthion (9).

Aphis gossypii Glover.—The cotton aphid is widespread and attacks seedlings and older plants late in the season. Natural enemies often give effective control but, where insecticides are necessary, nicotine and BHC have been added to the other materials used against cotton pests.

Organic phosphorus compounds are well known to be effective against aphids. TEPP give a rapid kill of the cotton aphid but was not persistent [Ivy & Ewing (98); Calhoun & Smith (28)]. A 1 per cent parathion dust was

also highly effective and superior to various chlorinated hydrocarbon insecticides [Loden & Lund (115); Gaines & Dean (72)]. It may be added to lime-free calcium arsenate at 0.5 per cent, and the mixture will then control the bollworm and the boll weevil as well [Hanna & Gaines (90)]. Methyl parathion is effective when applied at weekly intervals [Fife & Walker (66)]. Parathion should be used at 0.1 to 0.25 lb./acre and methyl parathion at 0.25 to 0.5 lb./acre (9).

Schradan was effective as a seed application, as a spray or when watered on to the soil and gave long-lasting protection [Ivy *et al.* (99)] Demeton gave a good control of aphids at 0.25 lb./acre which lasted for at least eight days [Davis, Cowan & Parencia (44)]. In Peru sprays and applications in the irrigation water were effective against aphids and several other cotton pests [Simón (153)]. It is recommended against the cotton aphid at 0.125 to 0.4 lb./acre (9). EPN only gave control at over 2 lb./acre [Scales, Ivy, Gaines & Rainwater (146)]. Chlorthion was effective at 2.5 to 3 per cent in dusts and also in sprays [Fife & Walker (66); Pfrimmer & Gaines (131, 132)]. Guthion is recommended at 0.25 to 0.5 lb./acre (9).

The disadvantage of many of the organic phosphorus compounds is their high toxicity to predators and parasites of cotton pests. Various Coccinellidae, Lygaeidae, and Nabidae placed on plants dusted with 0.1 lb./acre parathion and 0.2 lb./acre EPN were nearly all killed [Campbell & Hutchins (29)]. Aphids which had been fed on demeton-treated leaves were toxic to larvae of most Syrphidae tested, to some species of Coccinellidae but lacewing larvae were apparently nearly immune [Ahmed *et al.* (1)].

Thysanoptera.—Thrips of various species (*Frankliniella* and *Thrips*) are widely distributed. They attack young cotton and can cause loss of crop or delay in fruiting. Insecticides may control thrips without increasing the yield of cotton. DDT, BHC, and aldrin are effective.

Parathion gave very good control as a 1 or 2 per cent dust in the United States [Gaines *et al.* (75)] and in Egypt [Ghabn (79)]. EPN was effective at 0.08 to 0.125 lb./acre but has less residual action than toxaphene [Gaines *et al.* (75); Parencia & Cowan (126)]. It is recommended at 0.25 lb./acre (9). Demeton and malathion were effective at 0.25 lb./acre but not very persistent. Schradan was less effective [Gaines *et al.* (75)]. Thimet and Am. Cyanamid 12008 seed treatments have given effective control of thrips and other pests [Hanna (89); Parencia *et al.* (128)]. Guthion is recommended for use at 0.25 to 0.50 lb./acre (9).

Psallus seriatus (Reuter).—The cotton fleahopper is probably most effectively controlled by the chlorinated hydrocarbon insecticides, which kill nymphs and adults and have a good residual action. Control of this insect is often obtained incidentally with that of other pests.

Several organic phosphorus compounds have been tested but, although some were relatively effective, they show no special merit. HETP dust was toxic but not persistent [Ivy & Ewing (98)]. Parathion gave control

lasting about four days [Gaines & Dean (72)]. Schradan was only effective at high dosages [Ivy *et al.* (99)]. EPN at 0.125 lb./acre gave good immediate control but was inferior in persistence to toxaphene, DDT, BHC, and endrin [Parencia & Cowan (126)]. It is recommended at 0.25 lb./acre (9). Seed treatments with Thimet give limited protection of young plants [Parencia *et al.* (128)].

Calidea dregii Germar.—This polyphagous pentatomid attacks cotton, sorghum, and sunflower, among other plants, in Tanganyika and Urambo doing damage to the seed. In laboratory tests 0.05 per cent parathion was just inferior to pyrethrum powder, about equal to 5 per cent DDT and superior to BHC and aldrin [Duerden & Evans (56)].

Dysdercus peruvianus (Guérin).—This cotton stainer, which is a very injurious pest in Peru, was effectively controlled by parathion. In the same investigation it was found that *Aphis gossypii; Bucculatrix thurberiella* Busck, the cotton leaf perforator, and *Anomis texana* (Riley) were also controlled. It was necessary to add aldrin to kill *Anomis vestitus* (Boheman), which was the most serious pest [Wille, Simón & Gonzáles (178)].

Horcias nobilellus (Berg).—This mirid, which attacks cotton in Brazil, was killed by an 0.25 per cent parathion dust and, where the plants were heavily infested, the yield was increased [Lepage & Gianotti (112)]. *Lygus* spp. and other mirids can be controlled with 0.5–1.0 lb./acre parathion or malathion (9).

Tobacco

Tobacco is grown in many parts of the world; the most important producing countries are the United States (28 per cent), followed by China, then the U.S.S.R., and India, in that order. Smaller amounts are produced in about 50 other countries. Tobacco has a high value per acre and is extensively treated with insecticides.

Epitrix hirtipennis (Melsheimer) and *E. cucumeris* (Harris), the tobacco and potato flea beetle respectively, are both serious pests. The attack may occur in the seed bed or later in the field. Reference should be made to the paragraph on *E. cucumeris* under potatoes. Parathion, malathion, and demeton have all proved inferior to the various chlorinated hydrocarbon insecticides. When added to the transplanting water for tobacco plants, demeton controlled the beetles and reduced the number of leaf punctures; its use seemed promising, though Isolan was superior [Dominick (51)].

Protoparce sexta (Johanssen) and *P. quinquemaculata* (Haworth), the tobacco and tomato hornworm respectively, probably do more damage to tobacco than any other pest in the United States. By eating large quantities of leaves the huge larvae cause an estimated annual loss of crop worth over 84 million dollars. Control may be by hand picking or by insecticides; TDE and endrin are recommended. Parathion may be added to TDE to control aphids [Allen *et al.* (2)]. Alone, 1 per cent parathion dust gave only about 50

per cent control of fourth and fifth instar larvae and was inferior to DDT and toxaphene [Dominick (50)]. In laboratory tests of 13 compounds, parathion was second only to endrin and its ineffectiveness in the field was probably due to its short residual action. Malathion was inferior to parathion [Chamberlin (30); Guthrie (83)].

Heliothis virescens (Fabricius).—The larvae of the tobacco budworm eat into the buds at the growing tip and in certain areas such as Florida and Georgia they are the most serious pest of shade-grown tobacco. Parathion at 1 per cent and methyl parathion and Potasan at 2 per cent were all unsatisfactory [Chamberlin (31)].

Myzus persicae (Sulzer).—The green peach aphid, may develop on tobacco in sufficient numbers to cause serious stunting.

The organic phosphorus compounds are effective against these aphids and have often given control when applied only to the upper surfaces of the leaves although the aphids are concentrated on the lower surfaces.

A 1 per cent parathion dust gave complete control in shade-grown tobacco and even 0.5 per cent was very effective whereas 3 per cent nicotine dust was ineffective [Creighton & Gresham (35)]. At 1 per cent a weekly application is sufficient but at 0.5 per cent two applications per week are necessary. Parathion in conjunction with DDT for hornworm control was used on almost every Florida-Georgia shade-grown tobacco crop in 1949 [Chamberlin (30)]. It may also be used with DDT without causing plant damage [Dominick (49, 50)]. When necessary, parathion is effective on burley tobacco, but the need for a less toxic compound was felt [Bousch, Starks & Thurston (20)]. In the Belgian Congo parathion at 0.27 lb./acre has proved superior to DDT and nicotine. It was more effective as a spray than as a dust but the latter was preferred under local conditions [Vekemans (166)].

More recently investigations in Florida with shade-grown tobacco have shown that at 10 to 12 lb./acre a dust containing 1 per cent parathion gave excellent control. On flue-cured tobacco also a 1 per cent parathion dust was effective. As a spray 0.25 lb./acre of parathion was excellent. Malathion at 5 per cent in dusts was equally effective on shade-grown tobacco, while on flue-cured tobacco the 4 per cent malathion dust tested and sprays giving 1.0 lb./acre active ingredient were outstanding [Guthrie, Rabb & van Middelem (84)].

Detailed recommendations have been given for the control of the green peach aphid on tobacco in the United States. The choice lies between parathion, which is most effective, and malathion, which is less hazardous. To control the other main tobacco pests DDT, TDE, or endrin may be added [Lawson & Chamberlain (110)].

There is space only to mention briefly the results obtained with other organic phosphorus compounds. TEPP sprays were effective if they wetted the insects but the persistence was of course poor [Dominick (49)]. In the investigations in Florida on shade-grown tobacco, 2.5 per cent Metacide, 5

per cent Diazinon, and 2.5 per cent Chlorthion all also gave excellent control. On flue-cured tobacco, sprays of 1.0 lb./acre of Chlorthion gave outstanding control [Guthrie *et al.* (84)]. On burley tobacco, 1 per cent Chlorthion dust gave 97 per cent control 48 hr. after application. Am. Cyanamid 12008 was rapid in action and persisted well [Boush, Starks & Thurston (20)]. Schradan at 2.5 lb./acre gave effective and lasting control in Rhodesia [Ripper, Greenslade & Hartley (140)]. Systemic insecticides, including schradan and demeton, have been tested in Italy [Tirelli (162); Perucci (129)]. In America, on burley tobacco, demeton was rather slow in action [Boush *et al.* (20)].

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INSECTICIDES FOR CONTROL OF ADULT DIPTERA[1]

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While the immature stages of dipterous insects are the most important agriculturally, the adult stage is the more important to man and animals through annoyance and disease transmission. In view of the broad aspects of the topic, definitions of terms are made to delineate the scope of this discussion. Insecticides will be considered as those chemicals which either produce death or restrict activites of adult flies.

Concepts of Insect Control

In its broadest sense, insect control may be defined as the influence of various factors in regulating some phase of insect activity. Applied chemical control of insects involves the intervention of man by the use of chemicals as the regulatory influences. Although activity reduction of beneficial insects may result in adverse control, the species to be discussed are not beneficial and the qualitative definition of control is taken as the application of chemicals as suppressive measures on some phase of insect activity antagonistic to man's interests.

The chemical control of all species of flies is a very broad field and the present paper deals only with species directly affecting man and domestic animals. Procedures and concepts developed in the past 15 years will be emphasized.

Although control can be defined qualitatively, quantitative standards are more difficult to set for the following reasons:

(*a*) Control may be considered from two viewpoints (i) the change produced in the intensity of a given problem and (ii) the end result desired, e.g., results are given as per cent reduction of an original population, and as the residual population.

(*b*) Common usage of adjectives to describe control indicates that, short of species eradication or complete elimination of the problem, the outcome is usually subjective and depends on the opinion of the investigator.

(*c*) The subjective criteria of control may shift with the problem, e.g., one level of insect control may be satisfactory for disease reduction but unsatisfactory for disease eradication.

(*d*) The criteria of control may depend on the competitive methods available, e.g., the temporary control of flies with space sprays is less satisfactory since the development of residuals.

[1] The survey of the literature pertaining to this review was completed in June, 1957.

(*e*) Finally, the criteria of control must be viewed in relation to independent factors such as initial population levels, rapidity and extent of replacement, and differences in environmental factors.

The concept of control in terms of degree of population reduction deals with the intrinsic effectiveness of a method but does not necessarily consider the desirability of the end results. Control based on the desirability of the end results, while subjective, does consider the size and complications of the problem and does adjust to the desirability of the end results in terms of shifting criteria and would therefore appear more practical. The initial and end results should be given in numerical quantities, so other investigators can establish their own subjective criteria.

The effects of the two viewpoints of control can be shown as follows: with a pretreatment index of 100, population reduction of 90 per cent gives a post-treatment index of 10, which will be assumed satisfactory as an end result. Given a pretreatment index of 1000, a 99.9 per cent population reduction would be needed for an index of 10.

Evaluation of Control

Variations in obtaining numerical data for evaluating control are limited apparently only by the number of independent investigators. Methods may be regulated by the following factors: (*a*) the mobility and habits of the insect species involved, (*b*) the action and application of the insecticide, (*c*) the type of control area involved, (*d*) the type of control desired, and (*e*) the time and manpower available. General standardized procedures may not be possible but where contrasting methods are used to evaluate insecticides applied in a similar manner against a common species for a common endpoint the investigator should attempt to analyze the effects of any new evaluation variants.

In the evaluation of insecticides against tsetse-fly populations, a variety of techniques, based primarily on landing and catching rates, have been devised. Hocking & Yeo (1) recorded catches of nonteneral males of the tsetse fly (*Glossina morsitans* Westwood) taken along 10,000 yards of definite paths through areas treated by aircraft sprays, whereas fixed paths of 1000 yards with two boys catching at fixed stations were used by Symes *et al.* (2) in studies on *Glossina palpalis* (Robineau-Desvoidy). Random sampling of areas by two boys catching *Glossina pallidipes* Austen from a black cloth screen for 2 hr. was used by Whiteside (3). While these methods approximate each other, effects of the variations cannot be fully evaluated.

Landing rate counts have been varied in evaluating aerial sprays for tabanid control. Howell *et al.* (4) led horses through the test areas and made counts on the animals at 5-minute stops. In a similar type of study, Brown & Morrison (5) used a black cotton cloth draped over card tables at fixed stations for evaluation purposes. A standardized attractant appears better than horses which vary in attractiveness. The comparison of results from the two methods, however, cannot be made since there are no data determining the sensitivity of the insect response to the types of attractants.

Even in the evaluation of control of the sheep ked, *Melophagus ovinus* (Linnaeus), Matthysse (6) parted the wool on both sides of the body in making counts, while Fairchild *et al.* (7) made counts on one side of the neck from the shoulder to the base of the ear.

The same diversity of evaluation techniques can be shown for other flies. The examples chosen only illustrate the difficulties in reaching more than generalized conclusions from the literature. Each study may be scientifically sound but the comparison of results between studies is clouded by the lack of any standardization in the evaluation techniques and the criteria of control.

Fly Control in Structures

House applications by individuals.—Space sprays, aerosols, and fogs, although generally limited in residual action, are valuable for use by individuals against dipteran insects in homes. For years pyrethrum and subsequently the lethanes and thiocyanates were the principal spray ingredients.

Although pyrethrum has fast knockdown action and low mammalian toxicity, its killing qualities are limited. In recent years several compounds such as propyl isome, piperonyl butoxide, sulfoxide, MGK 264 [Fales (8)] and sesamolin [Beroza (9)], have been found which act as synergists in increasing the effectiveness of pyrethrum-base space sprays. The work of Schechter *et al.* (10) in 1949 describing the synthesis of the pyrethroid-like compound allethrin has led to the production of similar compounds including furethrin [Matsui *et al.* (11)] and cyclethrin. While Fales (12) reports these compounds approximate pyrethrins in intrinsic toxicity, they are not as active as pyrethrins when combined with the synergists listed above [Gersdorff *et al.* (13, 14)].

The present trend has been to combine pyrethrum-synergist or thiocyanate mixtures with insecticides such as DDT, lindane, methoxychlor, BHC, chlordane, and Strobane to obtain fast knockdown and effective mortalities [Brown (15)]. Since 1946 space sprays have been modified as liquefied gas aerosols, originally using dichlorodifluoromethane (Freon 12), which produced high-pressure aerosols showing good effectiveness against house flies and mosquitoes [Lindquist *et al.* (16); Resnick & Crowell (17)]. Low-pressure aerosols followed, using trichloromonofluoromethane (Freon 11) for part of the Freon 12. The latter have met with favorable public reaction due to their convenienece.

Only limited use is made by the individual householder of other chemical controls for flies. In general, residual treatments require specialized equipment. Limited residuals against flies are available as insecticides in furniture polishes, floor waxes, and paints. These residues often show limited effectiveness since they are normally restricted in application [Lindquist *et al.* (18)]. For control of sandflies, Trapido (19) found painting of house screens with 5 per cent DDT in kerosene markedly reduced the biting annoyance of *Culicoides furens* Poey.

Large-scale house treatment.—Large-scale house treatments have been

directed principally against mosquito and sand fly vectors of disease. In 1941 Russell & Knipe (20) reported that workers in India obtained effective control of mosquitoes for one to three days by weekly treatments with pyrethrum space sprays in huts. In 1945 Senior-White *et al.* (21) found daily use of pyrethrum sprays in dwellings controlled *Anopheles fluviatilis* Giles. Pyrethrum treatments twice weekly in dwellings were inferior to bimonthly treatments with DDT residues, however, in controlling *Anopheles culicifacies* Giles [Senior-White (22)] and *Anopheles gambiae* Giles [Turner (23)].

DDT residual applications largely replaced pyrethrum sprays since the extended effectiveness of DDT allowed the treatment of many houses with limited control crews. Davidson (24) has outlined the uses and limitations of residual applications in an excellent discussion.

Although Metcalf & Wilson (25) showed equal deposits of pyrethrum gave higher knockdown of *Anopheles quadrimaculatus* Say than DDT, DDT was superior in residual action for periods longer than 3 weeks after application. In extensive field tests Gahan (26) compared deposits from DDT solutions and emulsions against *A. quadrimaculatus*. Both formulations gave satisfactory results. Emulsions were less irritating to apply, however, and were more economical.

The type of surface treated influences the residual action of the different type formulations. Parkin & Green (27) showed that, when DDT-kerosene solutions were applied on wallboard, part of the DDT was absorbed with the solvent resulting in reduced effectiveness. They proposed the use of more concentrated solutions to minimize this effect. Clapp *et al.* (28) found reduced effectiveness of DDT emulsions on linoleum, fresh paint, plastics, and waxed wood. Mud surfaces also showed high absorption.

With solvent loss through evaporation, DDT and other halogenated hydrocarbons may form supersaturated droplets which have reduced action against insects. These droplets, however, crystallize when disturbed by the action of the insects on the treated surfaces [Parkin & Green (29)]. Barlow & Hadaway (30, 31) found oil solutions of insecticides more available to insects than either emulsion or wettable powder deposits. Particle size is also important in effectiveness. Exposed on a series of deposits ranging in crystal size, *Aedes aegypti* Linnaeus picked up crystals in the 10 to 20 μ range most readily. The mass and shape of the crystals also influenced pick-up. These factors were more important with DDT, TDE, and methoxychlor than with the inherently more toxic compounds dieldrin and BHC.

The problems of absorption, supersaturation, and particle size have been largely overcome with wettable powder formulations. Although these types of formulations leave visible deposits on the treated surfaces, the dispersions are finding increasing use. Malaria control programs in underdeveloped areas today, for example, use wettable powder almost exclusively. Mud surfaces, however, still show sorption of wettable powder deposits [Barlow & Hadaway (32)]. DDT and dieldrin show quite rapid loss of effectiveness on mud whereas BHC, although likewise absorbed, continues to exert a fumigant action over a short-term period.

Lethal qualities of insecticides are influenced by their irritant or repellent effects upon insects [Kennedy (33)]. Hadaway & Barlow (34) found various mosquitoes responded differently to residual deposits of various insecticides. *Anopheles stephensoni* Liston left DDT deposits in 2 to 4 min. after the first contact and only deposits having particles of less than 10 μ produced marked mortalities. *Aedes aegypti*, also stimulated in 2 to 4 min., was killed by 10 to 20 micron-particle deposits as well as the smaller sizes. *Culex pipiens molestus* Förskal, activated in less than 2 min. by DDT, was not killed by any of the deposits. Direct contact with BHC deposits activated all these species in less than 2 min. but BHC vapors did not activate the mosquitoes until they had received a toxic dose. Chlordane, aldrin, dieldrin, and toxaphene did not activate *A. stephensoni* in less than 25 min. Only toxaphene failed to effect complete mortality under the test conditions.

Since the feeding and survival of the insect hosts influence disease transmission, factors which alter either phase have been evaluated in field studies. Thompson (35) stated that DDT-kerosene residues in mud huts activated *A. gambiae* adults so they escaped without receiving lethal exposures. Sorption of the residues by the mud walls, however, might also have influenced the results. Wilkinson (36) also working with *A. gambiae* found that in wood-fiber board huts, deposits of DDT and BHC both gave 97 per cent mortality. In mud huts DDT produced 62 per cent mortality, while BHC continued to give 97 per cent mortality. With *Anopheles funestus* Giles, he found DDT and BHC in wooden huts produced 100 and 97 per cent mortalities and in mud huts 78 and 93 per cent, respectively. Colless (37) treated parts of the wooden walls of a house with DDT-kerosene, with kerosene alone, and left parts untreated. All treated surfaces repelled *Anopheles balabacensis* Barsas for 3 to 4 months but did not prevent biting. Residues from a DDT suspension killed some mosquitoes, drove some out before feeding, but still others completed feeding and left unharmed. Wharton (38) found DDT deposits did not reduce the feeding of *Anopheles maculatus* Theobald and gave nightly mortalities of only 63 per cent. For a four-week period, however, BHC prevented feeding and produced complete mortality. Against *Culex fatigans* Wiedmann, DDT reduced feeding about 45 per cent but effected no mortality. BHC reduced feeding only 27 per cent but killed all the adults for a two-week period.

Thus it is evident that an interplay of factors influencing the type and quantity of residual deposits, the type of surface treated and the reaction of the test species determines the outcome of residual control of the adult insects.

Many articles attest the success of the residual applications in controlling the mosquito species or their disease vectoring problem. Symes & Hadaway (39) state that in British Guiana deposits of 100 mg. DDT per sq. ft. reduced *Anopheles darlingi* Root in houses 99 per cent and inhibited the overnight feeding markedly. Subsequent results of the campaign led to the eradication of *Anopheles darlingi* and *Aedes aegypti* so that Giglioli (40) evaluated the duration of treatments by releasing the two species in the

area and by checking for possible re-establishment. In Venezuela, *A. darlingi* was practically eliminated, but *Anopheles albitarsis* (Lynch Arribálzaga) and *Anopheles albimanus* Wiedemann population densities were not affected. Nevertheless, the eradiation of malaria from a large part of the country has been reported [Gabaldon & Berti (41)]. Dowling (42) stated that BHC and DDT were both tried initially in Mauritius in 1949. BHC was dropped in 1950 because of short residual effectiveness. *Aedes aegypti* was eliminated in 1949, *Anopheles funestus* in 1950 but small numbers of *Anopheles gambiae* still persisted in 1952. Kraan (43), reporting malaria control in Holland, states that 5 per cent DDT solutions were replaced by 3 per cent DDT in combination with 3 per cent coumarone resin following the work of Van Tiel (44). Applications were made against *Anopheles maculipennis* Meigen only in the houses of healthy "carriers" of malaria (children with enlarged spleens).

The continued use of halogenated hydrocarbon residuals, however, has been clouded by the appearance of resistant strains of insects. Resistance in insects of public health importance has been reviewed recently by Busvine (45) and Quarterman & Schoof (46) who discuss mosquito species now resistant to DDT, dieldrin, chlordane, and BHC. The organic phosphorus insecticides, however, may find future use in the residual spray programs. Ludvik (47) has shown with topical application on *A. quadrimaculatus* that malathion and allethrin were more toxic than any of the halogenated hydrocarbon insecticides tested.

In controlling sandflies, applications of 5 per cent DDT-kerosene solutions at 200 mg. DDT per sq. ft. in houses have given excellent control of *Phlebotomus papatasii* Scopoli, *Phlebotomus major* Annandale and *Phlebotomus chinensis* var. *simici* Nitzulescu for 50 to 60 days in Palestine [Jacusiel (48)] and of various *Phlebotomus* spp. in Peru [Hertig & Fairchild (49)].

The use of space sprays, aerosols, and poison baits has not been developed in extensive control programs involving house treatments.

Treatment of animal shelters.—The control of flies in dairy barns and animal shelters is not only necessary from a health standpoint but also results in greater milk and beef production. Chemical control has been confined primarily to residual treatments, space sprays, or poison baits. Residual treatment of animal shelters is also equally necessary for malaria control wherever vectors with human blood meals tend to seek animal shelters for resting.

Residual treatments of large animal shelters, although generally requiring power spray equipment, have the advantage of extended residual effectiveness. Originally in 1945, Lindquist *et al.* (18) in detailed laboratory tests showed that DDT residual deposits were long-lasting and effective against the house fly, *Musca domestica* Linnaeus. In addition to the control of house flies in animal shelters, DDT residual deposits have also provided the best control of the stable fly, *Stomoxys calcitrans* Linnaeus. Methoxychlor has provided effective kills of stable flies [Eddy & McGregor (50); Muma &

Hixson (51)], while Diazinon has been the best of the organic phosphorus group with control lasting for 30 to 35 days [Dahm & Raun (52); Wingo (53)]. Baker & Schwartz (54), studying blow fly control with DDT, showed that a dosage of 200 mg. DDT per sq. ft. applied only to the observed daytime resting surfaces gave approximately two weeks' control. However, when nighttime resting surfaces were treated also, up to three months' control was obtained. These studies stress the importance of a basic knowledge of insect behavior in increasing the effectiveness of chemical control. Studies by Kilpatrick & Quarterman (55) and Maier *et al.* (56) describe in detail the resting habits of urban and rural fly populations under various conditions in relation to chemical control.

Although DDT failure against resistant fly strains was apparent in 1947 and 1948 in limited areas, it did not become almost universal in treated areas until several years later. DDT resistance was followed shortly by failure of chlordane and BHC residues to control house flies. With recognition and acceptance of the resistance problem, extensive studies were initiated to develop new means and methods for controlling resistant house flies. Pimentel *et al.* (57) described a method in which screen strips saturated with dieldrin and festooned from the ceilings of dairy barns and animal shelters provided highly attractive resting surfaces and remained effective for an entire fly season. Fly resistance to dieldrin soon rendered this method ineffective.

With widespread house fly resistance, a search began for synergists that would reactivate the halogenated insecticides, especially DDT [March *et al.* (58)]. Tsao (59) found that a nontoxic chlorinated polyphenyl increased the residual efficiency of lindane by retarding volatilization. Goodwin & Schwardt (60) sprayed 172 barns in 1952 with many possible synergistic combinations without finding a single effective formulation. Kilpatrick & Schoof (61) showed that a Dilan-DDT-cottonseed oil mixture effectively controlled resistant house fly populations. Kilpatrick (62) found cotton cords impregnated in a 10 per cent parathion-xylene solution when suspended from the ceilings of animal shelters provided season-long fly control with one application. Further studies with impregnated cords are described by Maier & Mathis (63), Kilpatrick & Schoof (64) and Schoof & Kilpatrick (65).

Organic phosphorus residual treatments against house flies have provided various results depending on geographic and climatic conditions, and method of evaluation. Sugar added 2.5:1 to Diazinon, malathion, Dipterex, Chlorthion, and Am. Cyanamid 4124, greatly enhances their residual action. Hoffman & Cohen (66) obtained only two weeks' control with Diazinon, Chlorthion, Bayer 21/199, and Dipterex. Hansens & Scott (67) obtained 40 to 50 days' control with Diazinon and Pirazinon, and Hansens (68) obtained 5 to 7 weeks' control with Diazinon, malathion, Am. Cyanamid 4124, Chlorthion, Dow ET-14, and Dow ET-15. Similar results were obtained by Goodwin & Gressette (69) and Kilpatrick & Schoof (70).

Although organic phosphorus compounds have their place in fly control, their use involves two difficulties; namely, initial cost and limited residual effectiveness. So far house flies have shown little resistance to organic phosphorus compounds. However, Keiding (71) reported resistance to Bayer 21/199 (Resitox) in Denmark.

Either parathion or Diazinon or both impregnated in cords have shown effective control of house-fly populations in dairy barns, rural areas, chicken ranches and military dining halls [Kilpatrick & Schoof (64)] for an entire season with only one installation per season. Cords have been used in dairies for a period of five years and commercially on a wide scale for two years with no known development of resistance. The total cost of treatments using commercially prepared cords is one-half to one-third that of the cheapest residual spray treatment presently effective and one-fourth the cost for season-long control. At the present time in terms of economy and efficiency, insecticide impregnated cords which have been registered for use in dairy barns, etc., by USDA are the residual treatment of choice for use in buildings housing animals.

Some of the early materials used in poison baits were a mixture of formalin in lime water, and sodium arsenite, pyrethrum or derris dust placed in fermenting materials. Although these toxicants reduce fly populations, they do not provide acceptable present-day control.

Thompson *et al.* (72) showed that 0.3 and 0.6 per cent lindane molasses baits were less effective than a 0.15 per cent lindane plus 0.06 per cent TEPP molasses bait. A combined lindane-TEPP bait also provided good control of horn flies when cows were left in the milking barn for 1 hr. or more. A 0.06 per cent TEPP bait provided house-fly control but did not reduce the horn-fly populations.

A new concept in dispensing of poison baits was devised by Bruce (73) who mixed a solution of 1.5 grams of Dipterex in 4 oz. of water with 1 pint of Karo syrup. The bait was painted on posts, window frames, strips, wires, and like fly-resting locations. Bait applied in June continued to kill flies in October with the best results on premises having good sanitation and effective screening. In 1954, Gahan *et al.* (74, 75) described effective malathion, Diazinon, and Dipterex bait formulations for the control of resistant house flies and demonstrated effective residual action of one to two weeks with dry bait formulations. Langford *et al.* (76), who tested 27 bait formulations, found malathion, Diazinon, and Dipterex to be the only promising materials. Keller *et al.* (77) found Phosdrin and Shell OS 1808 formulated in malt baits were more effective than malathion or Diazinon in controlling blow flies. DDVP, a new toxicant, [Mattson *et al.* (78)] produces spectacular reductions in house-fly populations in liquid baits [Kilpatrick & Schoof (79)]. A water bait of 0.1 per cent DDVP and 10 per cent sugar reduced a pretreatment fly count of 2000 in 3 hr. to a maximum count of 7.

In the rapid control of house-fly populations, poison baits can be much more spectacular than any other method; however, they do present certain

problems. Baits dispensed adequately and often enough give highly satisfactory control in most cases where the production potential is not excessively high. However, operators of dairies and like establishments tend to bring fly populations under control with baits and then to suspend treatments until a new high population has developed, resulting in a cyclic control of fly populations. Proper dispensing and location of baits and bait stations directly influence the degree of control obtained with any given formulation.

Until recently fly resistance to organic phosphorus baits had not been considered. However, Kilpatrick & Schoof (80) and Fay *et al.* (81) described a field strain of flies both physiologically and behavioristically resistant to all types of malathion bait formulations. Investigators are observing loss of control in other areas, indicating that a widespread problem may evolve, necessitating closer observations on fly behavior.

Temporary control of house flies and horn flies in animal shelters was attained by Morrison *et al.*, (82) with space sprays using DDT, pyrenone, and chlordane. Initially 5 per cent DDT space sprays in barns gave excellent control of house flies, but horn fly control occurred only when animals were left in the barn during treatment. DDT resistance of house flies forced a change in insecticides. Seventeen applications of a combination of 1 per cent piperonyl butoxide plus 0.1 per cent pyrethrum were required to provide satisfactory horn fly control for one season as compared with 11 treatments of 10 per cent chlordane to provide the same control.

Treatment of Commercial Structures.—The control of adult flies in restaurants, food processing plants, and in commercial transportation such as trains and aircraft is limited by rigid governmental restrictions as to the specific insecticides that can be used on the basis of toxicologic hazards including food contamination. Residual treatments have not been extensively employed for the control of flies and mosquitoes primarily because of the type of surface available for treatment or the danger of food contamination during application or through translocation. Sampson (83) reported that DDT or chlordane applied to areas of a cannery most frequented by adult flies gave highly effective control of house flies and the fruit fly *Drosophila melanogaster* Meigen. Block (84) used paint applications of 20 per cent DDT urea-formaldehyde resin to building surfaces without the danger of contamination. House flies exposed to the paint showed 50 per cent knockdown in less than 10 min.

Searles (85) applied the Dilan-DDT-cottonseed oil formulation (62) to preferred fly resting surfaces in milk products processing plants with brushes and obtained very effective control of house flies. Madden *et al.* (86) sprayed 5 and 20 per cent DDT-kerosene solutions on the interior of aircraft, and obtained 80 per cent knockdown of flies for six weeks or more. DDT (50 per cent) dust gave 42 per cent knockdown for two weeks on metal and 100 per cent mortality for six weeks on fabric. Pimentel & Klock (87) treated baggage compartments on aircraft with 200, 70, and 50 mg. lindane per sq. ft. and obtained 5, 3, and 1 weeks' control, respectively.

Aerosols have found wide use in many food establishments, and in ships, aircraft, and trains in international travel. Most aerosol formulations have pyrethrum as the base toxicant with additives such as piperonyl butoxide, MGK 264, and others. Fairclough (88) described the control of tsetse flies on trains with a Swingfog thermal generator. Fogs of 15 per cent DDT plus 0.05 per cent pyrethrum directed at one side of an open train provided an 80 per cent reduction of the flies.

The use of insecticide vapors for fly control has been restricted by the toxicologic aspects of inhalation of the vapors and by possible contamination of foodstuffs. In general, lindane has been used almost exclusively in vaporizers; however, Steiner (89) had good results with technical methoxychlor in high capacity heat vaporizers. High mortalities of flies and mosquitoes with exposures of 1 hr. or less occurred when the air in rooms passed through lindane impregnated filters [Sullivan (90)]. The treated filters were still effective after two months. Fulton *et al.* (91) showed that despite varied concentrations of lindane from commercial vaporizers and air circulation house flies were all killed within 3 hr. in ventilated test rooms. Quarterman & Sullivan (92) evaluating lindane filters in aircraft ventilating systems, found 30-min. exposures of free-flying flies to the lindane vapors produced 98 per cent mortality.

Fly Control on Animals

Application of insecticides to domestic animals for adult fly control can best be viewed on a fly species basis since considerable differences exist in the habits and methods of attack of the various species. The resting and biting habits of the horn fly, *Siphona irritans* (Linnaeus), largely invalidate the use of residual applications in animal shelters. Certain insecticides, such as lindane and Diazinon, however, exert a fumigant action from residual deposits and show the ability to translocate onto unsprayed surfaces, possibly to the animals themselves. Hansens (68) noted that numbers of horn flies and stable flies per animal dropped markedly in 1 hr. when cattle entered a barn treated the previous day with Diazinon. With cattle in barns 2 to 3 hr. daily, adult horn fly counts dropped from 98 to 4 flies per animal the first day, to 18 flies per animal for two weeks, and no retreatment was needed for 60 days.

Matthysse (93) obtained control of horn flies on range cattle for two to four weeks using 1 per cent suspensions and 2.5 per cent emulsions of DDT, but the wettable deposits retained effectiveness better where rain was a factor. Laake (94) tested 0.2 per cent DDT suspensions and 0.1 per cent DDT dips and observed increasing length of residual effectiveness with repeated treatments. With applications of 0.5 per cent wettable powders on cattle, DDT was the most effective compound giving more than 90 per cent reduction of adult horn flies for a two to three week period. In 1954, De Foliart (95) found applications of both 0.5 per cent wettable Dilan and DDT gave four weeks' protection against horn flies, and were superior to dieldrin, heptachlor, ethyl-DDD, and toxaphene.

Emulsion sprays of 1 per cent pyrethrins, 1.72 per cent cyclethrin or 1.72 per cent allethrin, each in combination with 10 per cent piperonyl butoxide, gave 70 to 80 per cent control of horn flies for periods of 5 to 12 days [Moore *et al.* (96); Granett & Haynes (97)]. Granett & Hansens (98) checked the effectiveness of 0.5 per cent methoxychlor emulsions alone and with 5 per cent butoxy polypropylene glycol and found the latter formulation more effective. Dust applications of 50 per cent methoxychlor wettable powder applied along the back line gave three weeks' control of horn flies [Lindquist & Hoffman (99)]. DeFoliart (100) tried dust applications of 50 per cent DDT wettable powder, 25 per cent dieldrin wettable powder and 1 per cent dieldrin dust and obtained two to three weeks of control.

Rogoff & Moxon (101) discuss the usefulness of cable-type back rubbers of insecticide saturated burlap for self treatment by range cattle. Oil solutions of insecticides were more effective than emulsions. Five per cent insecticide-oil solutions in decreasing effectiveness were DDT, methoxychlor, Dilan, and toxaphene. Lindane tested in 0.5 per cent oil solution was inferior to the other insecticides. Using 5 per cent DDT or chlordane solutions, Lindquist & Hoffman (99) found one treatment of the burlap lasted 30 to 70 days. Raun & Casey (102) found oil solutions of 4 per cent methoxychlor or DDT alone or in combination with 8 per cent butoxy polypropylene glycol gave 95 to 99 per cent control of horn flies over a five-week observation period. Control of the stable fly, however, was not satisfactory.

Bruce (103) developed a method for self treatment where cattle moving through a covered chute operated a treadle sprayer. Granett *et al.* (104) tested variations of sprayers and formulations and found satisfactory reductions of flies if cattle were treated once daily. Combinations of pyrethrum, piperonyl butoxide, cyclethrin, Thanite, lethane, and butoxy polypropylene glycol were used in these tests.

The inclusion of 100 p.p.m. lindane in diets fed to cattle gave control of horn flies for 21 days following treatment [Eddy *et al.* (105)]. Effects on stable flies and *A. aegypti* mosquitoes, however, were less evident.

Stable flies have not been as susceptible to insecticide application on the animals, probably reflecting their habits of resting on objects other than the host animals. While residual applications on their resting areas have been somewhat effective, poison baits have had essentially no action against this species.

Animal treatments for the control of tabanids has met with limited success. Goodwin *et al.* (106) found that Pyrenone 1 to 10 emulsions reduced counts of *Tabanus quinquevittatus* Weidman on horses about 90 per cent over a five-day observation period.

Insecticide application on the animals is obviously the best method of approach in the control of the sheep ked, *Melophagus ovinus*. Matthysse (6) found DDT dust applications inferior to rotenone dusts in immediate effectiveness. The dust applications were less effective than were dips. Fairchild, *et al.* (7) found dipping of sheep in 0.2 or 0.5 per cent suspensions of wettable DDT, methoxychlor, BHC, DDD, toxaphene, and chlordane gave nearly

complete control for a three to four month period. Hoffman & Lindquist (107) found high pressure applications were essential for control on long fleece sheep and that wetting agents improved the effectiveness of the insecticides. Muma *et al.* (108) gave an excellent review of control methods and evaluation procedures of the sheep ked. Comparisons with a DDT-sulfur suspension showed the method of application to be as important as the insecticides employed. Pfadt *et al.* (109) obtained marked reductions of the keds with two dust applications of 0.5 per cent rotenone or 1 per cent dieldrin at three-week intervals.

Cattle have been sprayed to prevent oviposition by the common cattle grub, *Hypoderma lineatum* (De Villiers) and the northern cattle grub, *Hypoderma bovis* (Linnaeus). Bevan & Edwards (110) applied 1 per cent DDT emulsion using 1 pint per animal on three occasions at two-week intervals during June and July, 1945. Results, based on larval counts made during January to July, 1946, showed approximately 90 per cent reduction of *H. bovis* but little effect on *H. lineatum*. Timing of the applications was proposed as the basis of differences in control. Raun (111) used automatic treadle sprayers and a spray of 10 per cent piperonyl butoxide with 1 per cent pyrethrins during the spring and summer of 1953. Effectiveness, measured by grub counts taken from December 1953 through March 1954, showed excellent control of *H. lineatum* and little control of *H. bovis*. Differences in the contact time of the fly with the host during oviposition was proposed as the reason for the differential control. Breev & Savel'ev (112) made seven or eight applications of 5 per cent DDT-5 per cent BHC emulsion per season and obtained control of the reindeer warble-fly *Hypoderma tarandi* (Linnaeus) on animal herds in the field.

Restriction of oviposition of the sheep maggot fly, *Lucilia sericata* (Meigen), was investigated by Stones (113) using dips of 0.5 per cent DDT suspension and benzene emulsion, 0.5 per cent DDT sprays and 5 per cent DDT dusts. The 0.5 per cent DDT suspension dip gave the best protection and exerted its action entirely against the adult flies.

Whiteside (3) explored the possibility of controlling the tsetse fly, *Glossina pallidipes* Austen, by applying 9 per cent DDT-9 per cent resin in groundnut oil on oxen and then pasturing the treated animals in specific areas. Treated oxen outnumbered the indigenous large wild game 6:1 but were fewer in number than the small game animals. With one spray weekly, the tsetse fly population was reduced 70 per cent in three months. With two sprays weekly, an 80 per cent reduction of the residual population occurred in two more months. Burnett (114) treated cattle twice weekly with 10 per cent DDT and used the animals at three times the number of wild game. He observed reductions of 99.5 per cent in *Glossima morsitans* Westwood and 92.5 per cent in *Glossina swynnertoni* Austen. Wilson (115) fed BHC to cattle to make them lethal to *Glossina palpalis* Robineau-Desvoidy. He found the cattle could tolerate 250 mg. per kg. on two days with additional doses of 125 mg. per kg. on the third and fourth days. The cattle were lethal to *G.*

palpalis for 41 days after treatment. A single dose of 250 mg. per kg. was lethal for 10 to 12 days.

In general, the animal treatments alone would probably not suffice for complete control of tsetse flies for the following reasons: (*a*) the tolerance levels between host survival and fly lethality are too close for practical purposes, and (*b*) the flies have many wild animal hosts available.

Area Fly Control

Aerosols, space sprays, and fogs have been widely used in municipal control of flies and mosquitoes. The effectiveness of these types of applications is influenced by the insecticide, the dosage and the particle size used, by the wind and the terrain and by evaluation techniques employed. In 1946, Brescia *et al.* (116) applied fog applications with a Besler steam aerosol generator and obtained good kill of adult *A. quadrimaculatus* and *Aedes* spp. 300 yards downwind in brush and 1 mile in open terrain when 10 per cent DDT-oil solution or emulsion was used at the rate of 15 gal. per 1000 ft. frontage. Effective control of *Anopheles farauti* Laveran for one to five days was accomplished by Brescia & Wilson (117) using a blanket treatment of 5 lb. of DDT per 1000 ft. of frontage dispensed in the form of a steam generated oil aerosol of 10 μ m.m.d. Dickerson *et al.* (118) showed that wind velocities of 8 m.p.h. appeared to be best using the TIFA aerosol generator. Brown & Watson (119) tested various aerosol generators and found the TIFA and Dynafog thermal generators were superior. Effective mosquito control was shown for 400 yd. downwind in either open or wooded areas. Chapman *et al.* (120), testing the effectiveness of insecticide sprays or fogs against salt marsh mosquitoes, found 2.5 per cent lindane the most effective followed by 2.5 per cent BHC, 2.5 per cent heptachlor, 5 per cent dieldrin, 10 per cent DDT, and 5 per cent chlordane. Baker & Schoof (121) controlled *Aedes sollicitans* Walker and *Aedes taeniorhynchus* Wiedeman at drive-in theaters with Swingfog applications of 1:1 fuel oil:kerosene solutions of 2.5 and 5 per cent DDT, 1 or 2 per cent chlordane, and with 0.25 per cent pyrethrins plus 2 per cent piperonyl butoxide. Application of the fog during or after the infiltration of mosquitoes at dusk was a prerequisite for effective abatement.

Evaluation of aerosol or space spray treatments is often determined by landing or biting rates. Factors influencing data from these techniques were studied by Smart & Brown (122) who found that *Aedes* spp. preferred warm to cool skin, dark to light skin, and dry to wet skin; thus, the person evaluating the treatment could bias the results.

The spontaneous and cyclic emergence of the blind mosquito, *Glyptotendipes paripes* (Edwards), in tremendous numbers has presented a serious annoyance problem. Lieux & Mulrennan (123) controlled the adults of this species with varying degrees of success using thermal aerosols of a DDT-oil solution and with BHC dusts.

Control of the sand fly, *Styloconops albiventris* DeMeijere was attained for four to five days by Brescia & Wilson (124) using 10 per cent DDT in oil

applied with a steam aerosol generator at dosages of 7 to 7.5 gal. per 1000 ft. of frontage.

Aerosols and sprays have been used as adulticides in the control of black flies. Goldsmith *et al.* (125) showed that aerial application of 0.5 lb. DDT per acre effectively reduced initial black fly populations but reinfestation occurred very rapidly. In large-scale test plots of over 100 acres, 0.35 lb. DDT per acre effectively reduced black fly infestations for 24 hr. but reinfestation began within 48 hr. Also small-scale tests with aerosols of DDT, pyrethrum, BHC, and a DDT-pyrethrum combination gave initial reductions for 15 min. only. Glasgow & Collins (126) controlled black flies with DDT-oil fogs using a thermal aerosol generator but reinfestation rapidly restored the population.

Area control of mosquitoes may be divided into complete area treatments and the use of barrier strips to protect a restricted area. Blanton *et al.* (127), using aerial sprays of DDT in chlorinated camphene-fuel oil solutions treated a 30 sq. mi. area at the rate of 0.1 lb. of DDT per acre. Although 90 to 95 per cent control was effected, rapid reinfestation made retreatment necessary within 7 to 10 days. In studies at Goose Bay, Labrador, Brown *et al.* (128) showed that aircraft sprays of 4.2 per cent DDT-oil solutions at the rate of 0.165 pounds DDT per acre gave 86 to 98 per cent reduction of mosquitoes and 50 to 80 per cent reduction of black flies. In 1951, Gerry (129), treating a heavy infestation of the midge *Tendipes decorus* (Johannsen) in Massachusetts through the use of DDT residual sprays on all vegetation adjacent to the lakes and ponds, was able to provide reasonable relief from this species. This control procedure has been continued for several years with satisfactory abatement.

In recent years, extended irrigation in agriculture has intensified mosquito problems. Portman (130) showed that *Culex tarsalis* Coquillett, *Aedes dorsalis* Miegen, and *Aedes nigromaculis* Ludlow could be controlled successfully in rural areas with airplane sprays of 2 per cent lethane 384 and 0.25 per cent dieldrin emulsions at the rate of 4 gal. per acre. In recent years certain flood water mosquito species have shown resistance to several of the halogenated hydrocarbon insecticides. In 1956, studies were reported by Gjullin & Peters (131) using airplane dispersed sprays of 0.47 lb. malathion per acre for the control of mosquito populations developing in a 2 sq. mi. area of irrigated land. Fifty-one per cent control was obtained of *Culex tarsalis* and 97 per cent control of *Aedes nigromaculis*.

Barrier strips have provided varying degrees of mosquito control. Johnson (132) sprayed a 900×180 ft. area with 6 lb. of DDT in 6 gal. of spray per acre. Populations of *A. farauti* dropped immediately but some reinfestation occurred within nine days. *Aedes vigilax* Skuse was drastically reduced and 38 days elapsed before reinfestation. In 1950, Ludvik (133) treated a 50-foot-wide barrier strip around a 22-acre area using a 5 per cent DDT-2 per cent resin emulsion at a dosage of 136 lb. DDT per acre. Almost complete elimination of *Anopheles quadrimaculatus* within the area was obtained. Quarterman

et al. (134) in 1955 were unsuccessful in preventing the infiltration of *Psorophora confinnis* (Lynch Arribálzaga) and *Psorophora discolor* Coquillett into an Arkansas town with a 400-foot barrier strip treated by an airplane with DDT emulsions. Dosage ranged from 1.2 lb. DDT per acre in the center of the strip to 0.35 to 0.74 lb. DDT per acre on the edges. Bidlingmayer & Schoof (135) obtained four to nine weeks' control of daytime annoyance from salt marsh mosquitoes by treating the vegetation and lower portions of outbuildings within a radius of 100 ft. from a dwelling with 5 to 10 lb. DDT per acre. DDT dusts have also been employed in barrier strips for mosquito control. Ponomavenko (136) used 5.5 per cent DDT dust applied at the rate of 90 lb. per acre in 22-yard strips for the control of *Aedes caspius* (Pallas). Complete protection was afforded for 10 days with very few mosquitoes recorded for 7 additional days.

Urban fly control programs have been conducted in numerous cities and towns using residual treatments to houses, alleyways, garbage cans, privies, etc. [Watt & Lindsay (137)]. Schoof (138) in Charleston, West Virginia, showed excellent city-wide control of house flies throughout the entire fly seasons from 1950 to 1952 with residual treatments of either DDT at 200 mg. per sq. ft. or dieldrin at 50 mg. per sq. ft. and with supplemental space spray treatments. In 1950 Burkhardt & Dahm (139) treated garbage cans and racks, back doors and walls along alleyways with 2.5 per cent DDT emulsion at the rate of 100 mg. per sq. ft. and obtained approximately 70 per cent control of fly populations.

Griffiths (140), using DDT aerial sprays dispersed monthly at the rate of 0.5 pound per acre, reduced fly populations in Manila to negligible proportions.

Quarterman *et al.* (141), using residuals of 400 mg. DDT per sq. ft. on marine grass deposits to control the stable fly, noted that the treatment killed adult flies ovipositing on the treated grass.

Residual treatments for the control of sand flies in Peru have been reported by Hertig & Fairchild (49). Deposits of 200 mg. DDT per sq. ft. from a 5 per cent DDT-kerosene solution, applied only to stone walls around houses, markedly reduced sandflies in the houses. Treatment of both the houses and walls reduced sandflies to extremely low levels for 12 to 19 months. Control was very localized since normal populations were found 75 to 200 yd. away from the treatments. Jacusiel (48) in Palestine, using 200 mg. DDT per sq. ft. on vertical outside surfaces for 50 m. around houses, failed to get control of *Phlebotomus papatasii* (Scopoli)

In area treatments for the control of tabanids, Gladenko & Fortushnyi (142) used talc or clay dusts of 6 or 10 per cent DDT, or 12 per cent BHC. At 4.5 lb. per acre, DDT did not give satisfactory control in talc dusts applied on vegetation. At 9 lb. per acre applied to plants in the early morning DDT gave good reductions for four days. A second application reduced tabanids to low levels for the season. DDT-clay dusts at 9 lb. DDT per acre gave sharp reductions of tabanids with no increase for 10 days. A second

treatment at 18 lb. DDT per acre reduced tabanids to a minimum level for the season. Brown & Morrison (5) in field tests with aerial applications of 0.5 lb. lindane per acre on 1 sq. mi. plots temporarily eliminated tabanids in open areas but not in the dense forest. DDT at 2 lb. per acre gave unsatisfactory reduction and dieldrin at 1 lb. per acre gave only slight control. Howell *et al.* (4) tested DDT, methoxychlor, toxaphene, and chlordane in cyclohexane-fuel oil mixtures on wooded 10-acre plots using each material at 2 lb. per acre, and obtained no marked control of tabanids.

The chemical control of tsetse flies in Africa has been extensively studied and evaluated by Hocking *et al.* (1, 143 to 148). In preliminary studies on densely vegetated islands in Lake Victoria, 0.2 lb. of DDT or 0.03 pound of BHC per acre as a coarse aerosol spray gave unsatisfactory results due to lack of insecticide penetration of the dense vegetation canopy. A fly-free corridor, 2×4 miles, through light deciduous scrub trees infested with tsetse flies was obtained using 4.6 per cent DDT in Shell Disoline applied at the rate of 0.5 gal. per acre. Seven treatments of coarse aerosol sprays were applied at two-week intervals. No *G. swynnertoni* were found for two months after the last spray. DDT at 0.2 lb. per acre or BHC at 0.03 lb. per acre in coarse aerial sprays on savannah woodlands were initially very effective in controlling *G. morsitans* and *G. swynnertoni*. Seven applications of coarse aerosol sprays at 0.25 lb. DDT per acre over a 90-day period gave eradication of *G. pallidipes*, 98 per cent control of *G. morsitans*, and 95 per cent control of *G. swynnertoni*. These levels of control persisted from 1950 to 1953 without further treatments. With seven applications of 0.25 pound DDT per acre applied at two-week intervals, *G. swynnertoni* was eliminated for a six-month period after the fifth application. The investigators concluded that coarse aerosol sprays of 0.25 lb. DDT per acre in savannah woodlands gave drastic reductions of *G. morsitans* and *G. swynnertoni* and complete eradication of *G. pallidipes*.

In Kenya, Wilson (149) showed that 5 per cent DDT sprayed on vegetation at 15 to 20 lb. DDT per acre gave dramatic tsetse fly control with complete eradication of *Glossina palpalis fuscipes* Newstead. Rupp (150) impregnated 20×55 inch black cloths with 3.3 gm. of DDT. Twenty-two cloths, hung on cords over a stream at intervals of 30 to 100 yd. for a distance of 1100 yd. reduced tsetse flies at the center point of treatment about 69 per cent for two and one-half months. Morris (151) using simulated animal traps covered with DDT-impregnated cloths, obtained high kills of tsetse flies at points of concentration. Symes *et al.* (2), with residuals of 100 mg. DDT or 11 mg. lindane per sq. ft. applied four times weekly, obtained 98 per cent control of flies at points of concentration.

In Zululand, DuToit (152) and Du Toit *et al.* (153) concentrated control efforts on tsetse flies in 200 sq. mi. of permanent breeding area and eradicated them from a 7000 sq. mi area. This study points the way for future chemical control of adult Diptera whereby basic ecology is supplemented by a variety of chemical attacks, preferably with different insecticides to minimize possible selection for resistance.

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FORAGE INSECTS AND THEIR CONTROL[1]

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Contrary to popular belief, forage entomology is not a new field of research. The development of DDT and modern methods of production and other low cost insecticides provided new and suitable weapons for those interested in the control of insects and other arthropods of forage crops. The high costs of milk production in the dairy areas of the United States and Canada plus the falling prices of beef in southeastern and southwestern United States provided added impetus to the production of low cost forages of top quality. Farmers reawakened to the value of good quality and quantity of forages and pasture. Good legume hay, if purchased on the open market, was no longer a cheap substitute for grain; grain was even more expensive. Progressive growers realized that the solution was to grow more top quality hay on their own farms as a substitute for grain. Increased costs, interest in quality and quantity of forages, new and more versatile insecticides all have contributed to a reawakening of interest in an old established field of entomology—forage entomology.

This review, because of space limitations, has been limited to a detailed examination of a few of the important insects of forage legumes. No space will be allotted to grasshoppers, which should be treated separately by a later Review. Similarly, no space has been allotted to billbugs, blister beetles, crickets, wireworms, armyworms, white grubs, white-fringed beetles, cutworms, sod webworms, corn and cereal insects or the insects of legume and grass flowers and seeds, all of which properly fall within the scope of forage insects and their control.

Insecticide residues are a limiting factor on the use of insecticides on forage crops. Tolerances have been established by the Food & Drug Administration under U. S. Public Law 518 for many insecticides for use on most vegetables and fruit. However, tolerances for insecticides on forage crops, except in a relatively few cases, have not been established. Without such tolerances, effective control measures and recommendations of them will continue to be hampered. On the other hand, much noteworthy research has been conducted on residues of forage crops and meat, milk and dairy products.

Potato Leafhopper

One of the most important pests of legumes, particularly of alfalfa, *Medicago sattiva* L., in the northeastern and mid-western United States, in Mexico, and parts of Canada, is the potato leafhopper, *Empoasca fabae* (Harris). In the United States, its range of distribution is limited mostly to

[1] The survey of literature pertaining to this review was completed, with one or two exceptions, in February, 1957.

the humid areas east of the 100th meridian. This line falls approximately between the 45 and 50 per cent relative humidity lines and marks the 40 per cent rainfall-evaporation ratio line. The insect does occur in the western United States at elevations below 4600 ft., wherever the annual rainfall is 25 in. or more with its resulting high average humidity (47, 48).

Potato leafhopper injury was prevalent for a long time before its cause was recognized (84, 180, 238, 260). It was not until 1927 and 1928 that the connection between alfalfa yellowing and the potato leafhopper was experimentally demonstrated [Jones & Granovsky (142); Granovsky (92)]. Much earlier, in 1896, Osborn (181) had reported its presence on potatoes; and Ball (16, 17) had demonstrated that leafburn of potatoes was associated with the feeding of the leafhopper. Later Ball (15) showed that *fabae* and *mali* were the same species, and indicated that the correct combination was *Empoasca fabae* (Harris). Following the classical work of Jones & Granovsky, Hollowell *et al.* (124) showed that the leafhopper was the cause of the yellowing and bronzing of clovers, *Trifolium* spp. Poos (198) and Poos & Wheeler (203) extended the list of host plants to well over 100 species.

The exact nature of the injury of the potato leafhopper has intrigued entomologists almost from the start. Early investigators believed that the yellowing and leaf curling was due to a virus transmitted by the leafhopper. Later it became apparent that a virus was not the causal agent but a localized toxin or enzymatic secretion was probably responsible for the symptoms (92, 172, 199). Granovsky (91) made microchemical tests which showed a greater accumulation of starch grains and sugar in the injured tissue. Histological studies showed a gradual disorganization and granulation of the plastids, clogging and isolation of vascular bundles of suberized or liquefied layers and complete disorganization of the phloem of the affected areas. Smith & Poos (225) concluded from histological studies that potato leafhopper injury was caused by mechanical plugging of the phloem which hindered the translocation of plant material from the leaves. In further work, Smith (224) found the sheaths which blocked translocation to be highly insoluble and of insect origin. Johnson (140, 141) girdled alfalfa stems with live steam and produced symptoms of yellowing which he concluded to be the same as those caused by leafhopper feeding. In later papers (138, 139) he compared normal alfalfa leaves and stems with leafhopper injured ones and found that the injured leaves were higher in dry matter, reducing sugar, total sugar, and total acid-hydrolyzable substances, but lower in total nitrogen. The reverse was true of the stems. He concluded that the clogging of the food conducting elements resulted in a higher concentration of the food in the leaves than in the stems. Medler (163) re-examined the nature of potato leafhopper injury, and stated that the clogging was not purely mechanical, but that the insect injects a toxin which causes hypertrophy of the affected cells characterized by nuclear enlargement. Such cells, he believed, might cause interruption of translocation and secondary symptoms of yellowing or reddening in alfalfa leaves.

In general (196) the symptoms of potato leafhopper injury on forage

legumes include the common tip and marginal browning, as well as conspicuous bronzing, purpling, reddening, and yellowing of the leaves and a reduction in flowering. Poos (199) tested 15 species of Homoptera commonly found on forage crops and only the potato leafhopper caused the typical injury just described. It is difficult to distinguish leafhopper injury from symptoms of boron deficiency (37, 38).

On older and less succulent plants, symptoms appear more gradually, but young seedlings may be killed outright in a few days by the feeding of one late instar nymph or adult leafhopper per leaf (92). Potato leafhopper injury, to legumes may result in loss of stand (97), loss in growth or yield (97, 137, 202, 222, 239), reduction in carotene (111, 138, 139, 165), and lowered protein content and grade of hay (202).

Beyer (21) had shown, at an early date, that the potato leafhopper breeds continuously throughout the year in Florida, overwintering on castor bean, *Ricinus communis* L. and poke weed, *Phytolacca americana* L. but early investigators (67, 80) believed that it hibernated and overwintered in the north as an adult. However, Poos (198) found no leafhoppers overwintering at Arlington, Virginia, and stated that the insect did not overwinter in the north but migrated north each spring. He (197) later stated that the leafhopper appeared in Arlington about May 7 going directly to oak, *Quercus* spp. and hickory, *Hicoria* spp. where they built up in numbers. Similarly, Delong & Caldwell (51) were unable to find or overwinter the potato leafhopper in Ohio. This concept of spring migration of the leafhopper is now generally accepted. However, studies are still in progress to further confirm the theory and to ascertain the route and timetable of the migration.

A detailed description of the potato leafhopper and its life history is presented in a number of papers by Osborn (180), Fenton & Hartzell (67), Ball (15), Poos (198), Delong (47, 50) and others.

Fluke (77) and others (49, 52, 61, 68) early discovered that bordeaux was useful in controlling the potato leafhopper on potatoes, but such treatments were not applicable for use on most forage crops. Dusting sulfur, pyrethrum and pyrethrum-sulfur dusts were the commonly used materials until the introduction of DDT and the other chlorinated hydrocarbons (18, 195). DDT, (194) and TDE (109) were highly effective for leafhopper control. These early tests with DDT on the potato leafhopper were instrumental in starting a re-evaluation of forage insect control. Since DDT residues were found to persist on hay (4, 45, 220, 281) and to appear in the butterfat of milk, work with other compounds BHC, methoxychlor, parathion, etc., was pursued with great vigor. At present, methoxychor used at the rate of 0.5 to 1.0 pound of active ingredient per acre applied either early as a protectant or later as a remedial treatment is recommended by most states. Parathion and malathion are other materials that are suggested (107).

Before the advent of reliable insecticides for use on forage, such practices as regulating the time of cutting (135, 222, 223) were largely advocated.

Early in the work on forage, certain varieties of alfalfa and clover were

found to be resistant or tolerant of leafhopper injury (134, 136, 171). Work on varietal resistance of legumes to potato leafhopper continues and some progress has been reported (100, 245). Wilson *et al.* (282), in a comparison of nine varieties of alfalfa under varying moisture levels, indicate that Ranger was more tolerant of leafhopper infestation when an adequate water supply was available. This was not true of the variety Buffalo. Much remains to be done on leafhopper resistance, and this field of research on forage crops remains largely untapped.

Spotted Alfalfa Aphid

While the potato leafhopper is an old established pest of legumes in the United States, a new pest of alfalfa which first appeared in the Southwest, the spotted alfalfa aphid, *Therioaphis maculata* (Buckton), is unquestionably now the most serious pest of alfalfa in that area.

The spotted alfalfa aphid, which is known to occur in India, Israel, Italy, and other Mediterranean countries (255) was first discovered in the United States in New Mexico in 1954 and soon afterward in Arizona and California. In 1954, Tuttle & Butler (256) described its injury and suggested methods of control. By 1955 (255) the insect was causing severe damage to alfalfa in the Southwest and had spread through 11 states. The aphid has continued to build up rapidly and spread. It is believed to have shown the greatest rate of spread of any pest ever introduced into the United States. By January 1, 1957, it was known to occur in 30 states in a more or less continuous belt from California to Virginia and to the Gulf States.

Dickson & Reynolds (55) and Dickson *et al.*, (54) reported that the spotted alfalfa aphid attacks alfalfa, *Medicago sativa;* bur clover, *Medicago hispida;* black medic, *Medicago lupulina;* and to some extent berseem, *Trifolium alexandrinum.* Most species of *Trifolium* such as white or red clover, birdsfoot trefoil, *Lotus corniculatus;* and vetch, *Vicia* were not suitable hosts.

The injury to alfalfa from the feeding of this *Therioaphis* is much more severe [Reynolds & Anderson (207)] than that resulting from attacks by other aphids. The spotted alfalfa aphid injects a toxin into the plant and small numbers may kill a plant. Painter (8) believes that the toxin may interfere with chlorophyl production, as there is an abnormal amount of leaf yellowing and leaf drop. Diehl & Chatters (56), using histological and cytological methods found that the insect feeds within the phloem and mesophyll parenchyma and that considerable quantities of saliva or some toxic substances are injected into these tissues. They found that the greatest damage occurred in the mesophyll where the toxins caused lysis of the cytoplasm that was evident macroscopically as chlorotic areas.

The spotted alfalfa aphid is responsible for several types of economic damage to alfalfa and loss. Heavy infestations which are allowed to persist often result in the cessation of growth, the death of many plants and the depletion of stand. The aphid secretes large amounts of honeydew which

covers the ground and the leaves and stems of the plants. This honeydew provides a good medium for the development of a black, sooty-mold fungus which often makes the hay unpalatable to livestock. When honeydew is abundant, normal harvesting of hay or seed is impossible, as machinery may become so sticky that it is necessary to clean it periodically and frequently normal baling is impossible (54). Estimates in dollars of losses caused by the spotted alfalfa aphid (6) computed from 11 states from California to Nebraska and Texas range from $4,840,000 in 1954 to $41,860,000 in 1956. These figures in some cases include losses resulting from drought.

According to Dickson *et al.* (54), the spotted alfalfa aphid, which at first was confused with the yellow clover aphid, *Therioaphis trifolii* Monell, of eastern United States is an ovoviviparous, parthenogenetic insect in southern California where alate and apterous females are present throughout the year. Between 9.3 and 21.4 days were found to be required from birth to maturity, and each aphid gave birth up to 3.6 young per day. In Oklahoma, the aphids spend the winter as apterous adults and as nymphs on and around the crowns of alfalfa, where they were able to maintain themselves at temperatures as low as 10°F. [Bieberdorf & Bryan (22)]. In Israel, Harpaz (113) reports that there are as many as 45 generations a year, some of which are as short as 6 days and others as long as 29, depending on the temperature and month of the year. He reported that some individuals produced as many as 115 young at the rate of 1.7 to 4.8 aphids per day.

T. maculata (Buckton) is easy to kill with insecticides, but commercial control is frequently difficult to maintain because of reinfestation from neighboring untreated fields. Demeton (2 to 4 oz. per acre), methyl demeton (4 oz.), parathion (2 to 4 oz.), malathion (8 to 16 oz.), Diazinon (11 oz.), endrin (4.8 oz.) and, in most cases, toxaphene (3 lb.) and TEPP (1 pint) plus DDT (1.0 lb.) have given excellent control of the aphid. As dusts, toxaphene (15 per cent) plus DDT (5 per cent) at 24 lb per acre gave excellent control. Normal applications of toxaphene or toxaphene-DDT dusts for *Lygus* control will, in most cases, hold the aphid in check [Reynolds & Anderson (207)].

Larval and adult ladybird beetles are probably the most important aphid predators, although *Geocoris*, *Chrysopa* larvae, *Orius*, *Nabis* and larvae of syrphid flies also prey on the aphid (54, 113). In California, three hymenopterous parasites, *Praon palitans* Muesebeck, *Trioxys utilis* Muesebeck and *Aphelinus semiflavus* Howard have shown good promise for aphid control and in many states in the west several species of *Entomophthora* fungus are also promising.

In the fall of 1954, the alfalfa variety Lahontan was found to have a high degree of resistance to the spotted alfalfa aphid. Subsequent studies indicated that 3 of the 5 parents of Lahontan (C-84, C-89 and C900) were also resistant (8). Work is now under way to determine if other varieties are as resistant to *Therioaphis* as Lahontan, which is not adaptable to all regions where the aphid has been found. Harvey & Hackerott (117) readily isolated

from Buffalo, plants which appeared to have a level of resistance comparable to that of Lahontan and which are more adaptable to the northern range of the aphid.

Alfalfa Snout Beetle

While the spotted alfalfa aphid represents an insect of recent introduction on forage crops which has spread rapidly across the United States, the alfalfa snout beetle, *Brachyrhinus ligustici* (L)., an insect widely distributed in central and boreal Europe, is one of early introduction, 1896, [Palm (186)] which has been maintained in two counties of northern New York. Herrick (123) first reported the alfalfa snout beetle from this country. Palm (184 to 187) Claassen & Palm (36) have presented the earlier work on the alfalfa snout beetle in the United States. Vassiliev (257) presents a good account of its activities in Russia and Palm (186) has reviewed the more important European literature.

The alfalfa snout beetle is a wingless, parthenogenetic weevil, having a two-year life cycle, which feeds on the foliage of alfalfa; sweet clover, *Melilotus* spp.; ladino clover, *Trifolium repens* L. and many other plants including weeds. The principal injury is caused by the white, legless grubs which feed on the roots of alsike clover; *T. hybridum* L., sweet clover; *Melilotus* spp., red clover; *T. pratense* L., alfalfa; birdsfoot trefoil, *Lotus corniculatus* L. and many weeds [Gyrisco & Palm (108)].

Most of the eggs are deposited in the upper 2 in. of soil close to the host plant. There is no consistent difference in the duration of incubation period at soil moistures of 3 to 13 per cent but the period is longer at 2.5 per cent moisture [Lincoln & Palm (152)]. The period is shortest at soil temperatures of 75° to 80°F. (9 to 10 days) and longest at 50°F. (74 days). The larvae feed at a greater depth in sandy than in gravelly or loam soils and are nearer the surface if the populations are great. They move down to hibernate in November and December when soil temperatures drop to 45°F. or less. Larval development stops at temperatures of 83°F. or higher and is retarded by those 60°F. or lower. Larvae will pupate without being first exposed to low temperatures but mortality is great. A small percentage of grubs do not pupate until the third summer resulting in a three-year life cycle. Pupation occurs first in light, well-drained soils and is correlated with soil temperatures in the spring. The pupal period varies from 61.1 days at 50°F. to 11.4 days at 85°F. (152).

Adults move upward through the soil about 10 days prior to emergence, after the soil has thawed, when the soil temperature reaches 44°F. (152) and adult migration begins when soil-surface temperatures reach 70°F. usually about late April in New York.

Oviposition occurs at temperatures ranging from 50° to 85°F. but the optimum range is from 75° to 80°F. The beetles oviposited on 21 different host plants when confined to these plants but the numbers of eggs laid varied greatly with the species. On broad-leaved dock; *Rumex* spp., white sweet

clover, *Melilotus alba* Desr., red clover; wild strawberry, *Fragaria* spp., and alfalfa the eggs laid per female ranged from 501.5 to 306.5 in that order. Eggs will not hatch at temperatures over 85°F. and many eggs do not hatch even under favorable temperatures [Lincoln & Palm (152)].

The larvae pass through seven instars (186, 257) although field mortality is high in case of dense populations with the feeding of skunks accounting for much of this mortality. Winter mortality of larvae may reach 75 per cent under certain conditions (152).

Direct control of the alfalfa snout beetle is best obtained with poisoned baits directed against the newly emerged adults on plowed, infested legume sod in late April or May. Fruit baits of raisins, dried peaches, apricots, prunes, figs, and dates mixed with wheat bran and sodium fluosilicate have proven very effective when pelleted through a food chopper and applied weekly at the rate of one bushel per acre for three weeks. Baits containing an insecticide plus both sugar and soybean flour as attractants and conditioners using crushed corn cobs or peanut shells as carriers have been standardized as the most effective alfalfa snout beetle baits [Palm *et al.* (188); Gyrisco *et al.*, (101)].

For a number of years sodium fluosilicate remained the standard insecticide in the alfalfa snout beetle bait formula, but later investigators (101, 106) showed that aldrin, dieldrin, chlordane hepachlor, isodrin, endrin, BHC and toxaphene were all superior to it for alfalfa snout beetle control. Thermal aerosol and mist applications of oil solutions and emulsions of aldrin, dieldrin, chlordane, toxaphene and BHC were found effective for treating infestations of alfalfa snout beetles [Muka *et al.* (174)] in forage. Fumigation of the soil with methyl bromide, dichloroethyl ether [Lincoln *et al.* (153)] or carbon disulffide is an effective eradication measure for treating new small, isolated infestations (153, 221). Aldrin, dieldrin, heptachlor, and chlordane, especially in a granulated formulation, show promise for control of the larvae [Muka (174a)].

Such cultural practices as clean culture, fall-plowing, frequent short rotations, seeding of uninfested ground and protection of uninfested alfalfa with baited furrows aid greatly in controlling the alfalfa snout beetle.

Alfalfa Caterpillar

A serious pest of alfalfa in the southwestern United States is the alfalfa caterpillar, *Colias philodice eurytheme* Boisduval. Here this insect, unlike in most of the United States, is an important pest of alfalfa by virtue of its enormous numbers which occur in this well adapted environment.

Early in the study of the alfalfa caterpillar it was noted [Wildermuth (280); Gerould (87)] that the adult butterfly was polymorphic. In general the orange race is found largely to the south and west, the yellow to the east and north. The white form which is a genetic variation in certain females occurring in the yellow and orange races is found throughout the region but greatest in numbers to the far north [Hovanitz (127)]. In nearly all regions

there is intermingling of the color forms; this frequently occurs even at extremes of their areas of distribution. Later, some excellent studies, principally by Gerould (85, 86) and Hovanitz (126 to 130) were made on this butterfly on its ecological color differences, genetic and seasonal color variations and hybridization of the three color phases.

Hovanitz (126, 127) pointed out the range of the various races was associated with their adaptability to various environments and that differences in distribution of the orange and yellow races are due to (*a*) diapause for winter hibernation in the yellow race, (*b*) food plant distribution of the orange and yellow races and (*c*) different physical environment preferences. Hovanitz (127) found that the orange and yellow races of *Colias* in North America interbreed readily to produce fertile hybrids in areas where they coexist. This occurs most often in localities where their respective food plants, clover and alfalfa, exist together in the same fields.

Oviposition [Floyd (78)] of the alfalfa butterfly begins 48 hr. after mating. The female lays her eggs singly, usually on the upper surfaces of the leaflets. Floyd found that the mean number of eggs laid was 353 and that oviposition extended for about 9 days. Hovanitz (127) found that female *Colias* make long flights and tend to congregate where proper legumes in very early stages of growth are found; egg-laying capacity may vary from 50 to over 700 depending on the availability of nectar for the adult females. It is imperative that egg laying commence soon after cutting so that the life cycle will coincide with the haying practices where hay is cut about every 30 days (127, 228). Eggs laid too late have little chance for maturity as many of the larvae and pupae are destroyed by haying. Under conditions (127) early in the season or late in the season, the growth rate of the alfalfa may be faster than that of the butterfly so it may be cut oftener than the broods of butterflies come to maturity.

The larvae pass through five instars and can complete their life cycle from egg to adult in three weeks at 77°F. (127). Floyd (78) found that a single caterpillar consumed an average of 57 leaflets of alfalfa during its larval period.

The lowest level of larval infestation (228) occurs after cutting and before new growth starts. The caterpillars remaining on the hay either pupate or are killed by the direct sunlight. Similarly if the pupae are not protected from the sun many of them will be killed. In the hot arid regions of the Southwest where heat-protected places for adults can be eliminated by destruction of weeds along drainage, irrigation ditches and roads will result in desiccation and sterilization of the adults. Such practices together with controlled and supervised time of cutting by neighboring alfalfa growers can reduce the number of adults infesting any one field (127). Such a practice of community action whereby control is supervised utilizing disease, parasites, predators, chemical control together with manipulations of the environment has resulted in effective control of the alfalfa caterpillar. It represents the fullest use of man's knowledge of an insect and its environment for control purposes.

Michelbacher & Smith (168) concluded that climate is the limiting factor in holding down populations of alfalfa caterpillars but *Apanteles medicaginis* Muesebeck is a very destructive and useful parasite of caterpillar populations. Since this parasite may be seriously harmed by chemicals and because natural factors are so effective against the alfalfa caterpillar, insecticides should be applied only on the basis of careful and adequate caterpillar population counts (227, 231). A supervised control program makes chemical control more effective by improving the timing of applications and eliminating unnecessary treatments which may merely injure the parasites.

Some of the early chemical control work was conducted by Wildermuth (278, 279, 280) who used pyrethrum flowers with rather poor results. He as many others later (27, 44, 62) concluded that cultural practices gave the best available control. Smith & MacLeod (229) used calcium arsenate-sulfur and sulfur alone with poor to fair results. Floyd (78) reported good results on fifth instar larvae using copper arsenate and calcium arsenate. Smith & Allen (227) found DDT and TDE to be effective at dosages as low as 0.15 lb. per acre and superior to most other chlorinated hydrocarbons and organic phosphates. However since DDT or TDE are not approved for use on hay by the FDA, most states are now recommending as a chemical control methoxychlor at 0.75 to 1 lb. per acre applied as an emulsion spray (70, 208).

Steinhaus (236), Steinhaus & Thompson (237), and Thompson & Steinhaus (248) in some classical work found that a polyhedrosis of the alfalfa caterpillar is an important factor in natural control of larval populations. However they found that naturally occurring epizootics of this virus disease cannot, in general, be depended upon to give satisfactory economic control as they usually occur only after serious damage to alfalfa has taken place. Transmission of the virus can occur by *Colias* adult contamination, insect parasites, carnivorous insects, and wind, rain, and irrigation water. If the infestations of caterpillars are found early, in the initial stage of development and growth, a well-timed application of virus suspensions made from virus killed caterpillars and applied at the rate of 10 cc. per acre or 1 pint per 50 acres will give good control and is recommended for alfalfa caterpillar control in California (208).

The Pea Aphid

The pea aphid, *Macrosiphum pisi* (Harris), was first noted as a serious pest in the United States about 1899, although it had long been recognized as a problem in Europe (57). Folsom (79), suggests that this insect was introduced from Europe, where it is widely distributed and is particularly common in England, Germany, France and Italy. The pea aphid in the New World has spread from where it was first destructive in the Middlewest and Atlantic seacoast area [Davis (43)] over almost all of the United States and southern Canada.

Apparently peas are the preferred food plant, although other crops such as alfalfa, vetch (53) and clover (79) are frequently seriously damaged. Folsom

(79) lists the following as the more important food plants: red clover; crimson clover; field peas *Pisium sativum* L.; vetches; lettuce, *Lactuca sativa* L.; shepherd's purse, *Bursa bursa pastoris* L.; and nettle, *Pipturus* spp., as well as many weeds of the legume family. Alfalfa serves as an excellent host under conditions which approach the optimum temperature of 65°F. and optimum relative humidity of 80 per cent in Kansas [Smith & Davis (226)]. As a result, this aphid is particularly a pest on alfalfa early in the growing season (230).

The pea aphid damages its host plant by sucking plant juices from leaves, stems, blossoms, and legumes, causing the plant to be wilted and stunted, and in addition these plants are often covered with numerous cast skins and honeydew.

Because of the variations among aphid populations a concise description of its life cycle is difficult to make. The pea aphid may overwinter as an adult or egg or both, depending largely on the winter temperature. Huckett (132) reports that in many sections of New York the aphid overwinters chiefly, if not entirely, in the egg stage on alfalfa and clover. In western Maryland [Ditman *et al.* (58)] the insect passes part of the winter in the egg stage although live aphids have been taken in December. In eastern Oregon and Kansas the pea aphid overwinters in the egg stage (44, 53) while in the southern part of the United States the pea aphid may continue to feed and reproduce during the winter. In areas where eggs are the overwintering form, they begin to hatch with the coming of spring and new growth; the date of egg hatch varies somewhat with the particular locality (44, 57, 79). The newly emerged aphids are all females and after 4 molts and a maturation period of 8 or 10 days give birth to an average of 39 young over a reproduction period of 12 to 31 days (44). Results of other studies show reproduction at a mean of 11 days after birth and an average total reproductive capactiy of 46 with a maximum of 147 (79). Campbell (25) reported an average production per female of 68 with a maximum of 28 generations per year and a minimum of 14, while Davis (43) reported a maximum of 19 generations and a minimum of 13. The aphid continues to reproduce parthenogenetically throughout the summer. Both winged and wingless females are produced; the production of the winged females is supposedly stimulated by crowding [Schaefer (214)].

The winged females are the chief means of spread and although they are feeble in flight, they are assisted by wind to increase their range (79). During the early part of the season the aphid feeds heavily on alfalfa and clover and as summer approaches migrates to annual legumes [Maltais (157)]. Evans & Gyrisco (64) report that the pea aphid may be classified as a migratory aphid and they also believe that the pea aphid exists in different forms (fundatrices, fundatrigenae, sexuparae, and sexuales). In September and October the aphid again appears more plentiful on alfalfa but seldom causes appreciable injury (44). In areas where the aphid overwinters in the egg stage, the last generation is composed of both males and females, which mate, and the females lay their eggs on the crowns of clover and other pri-

mary host plants [Maltais (157)]. Eggs are also often found on the leaves, stems, and even terminals of the host plant (79).

The pea aphid is the most important vector of pea viruses [Swenson (243)]. Swenson (244) reports that the alfalfa mosaic virus was transmitted most efficiently by *Aphis gossypii* Glover and *M. pisi*. Other workers have demonstrated the spread of yellow bean mosaic from red clover to beans by the pea aphid (41). Economic increase in yields have been obtained through the use of insecticides to decrease spread of legume viruses (132, 243).

Certain natural parasites and predators play an important part in the control of the pea aphid. Fluke (76) lists over 70 organisms which have some bearing on pea aphid populations. The fungus, *Empusa aphidis* Hoffman has been reported to kill large quantities of aphids under relatively humid conditions (79). Among the other important predators and parasites are the ladybird beetles, at least nine species of the family Coccinellidae, certain members of the family Syrphidae, lacewing flies, damsel bugs, two species of the family Nabidae, as well as many others.

A number of workers have reported the presence of strains of alfalfa growing in fields which were resistant to attacks of the pea aphid. Among the earlier were Blanchard & Dudley (23) and Painter & Grandfield (183). Since that time several researchers (114, 115, 143) have worked on various phases of resistance of host plants to the pea aphid. The possibility of the use of resistant varieties in connection with the control program is of significance, and one that is certainly worthy of further study.

Through the years many materials have been used for the control of the pea aphid. Among the ones that have been used successfully are cube powder (132), DDT (125), schradan (23a), BHC (5), rotenone (93), endrin, Metacide, parathion, demeton, EPN-300 (82), malathion (58), TEPP, and lindane. Because of residue limitations the number of insecitices which can be used is limited. At present, organic phosphate materials which include parathion, TEPP and malathion applied at 4 to 5 oz./acre are recommended in many states. Cultural practices have also been demonstrated to be valuable as a method of control (213) .

Alfalfa Weevil

According to Titus (250) the alfalfa weevil, *Hypera postica* (Gyllenhal), is widely distributed in the Old World being found wherever alfalfa is grown. He reports the weevil to be present throughout all of Europe, including Russia, except for the northernmost limits of that continent, in western Central Asia or the Near East, southwestern Siberia, the North Coast of Africa, and in a small area in India.

In 1956 (7) it was reported from 13 western states from New Mexico to North Dakota and west to Washington and California. It was first found in eastern United States in Maryland in 1951 (201) and has rapidly spread to nine other eastern states (7, 10, 204).

Damage is variable as the weevil occurs over a wide climatic range. In

some fields 30 per cent of the new spring growth had been killed (251) and young stands of alfalfa may be killed outright by migrating weevils (258). Spring feeding consists of the adults making punctures in the stalks whereas in the later feedings on the second and subsequent crops the weevils rasp the epidermis from the stalk and slit the leaves into ribbons (252).

Copulation of overwintering forms appears to be continuous from spring to fall and all during the oviposition period (189; 252). Reeves (205) reports that the alfalfa weevil has no definite period of hibernation and is quiet when cold and active when warm. Most weevils creep into crevices in the ground where they spend the winter. On warm days in winter the beetles can be found moving in areas where the snow has melted (156).

One of the most important considerations which has proven useful in control is the fact that a female emerging from the cocoon is not sexually mature. The length of the maturation period is variable and greatly influenced by temperature. Snow (232) found that the shortest time for the weevils to reach sexual maturity is at least 4 months while Yakhontov (285) gives the time of 55 to 60 days if the temperature does not drop below 12°C. or rise above 25°C.

The first egg laying in the spring is restricted to females that have reached sexual maturity the previous fall. Oviposition increases when daily temperatures average about 50°F. (112). The peak of egg laying occurs on the first crop. The eggs are laid in clusters in a characteristic circular hole made by the female in the living or dead stems. The number of eggs deposited in each stem cavity ranges from 1 to 45, with an average of about 9 (112, 169, 190, 205, 231, 251). One female may lay over 1500 eggs although the average is usually about 600 to 800 (110, 249). The incubation period for one lot of 1139 eggs varied from 7 to 16 days, with the average slightly over 10 days (251). The larva passes through four instars (112, 253) although some writers believed the larva to pass through a variable number of instars (156, 206). The larval period has been reported by various workers to range from 23 to 40 days (240, 253). Upon reaching maturity the larvae crawl to the ground where they spin a delicate net-like cocoon which is often partly enveloped by one or more leaves (63). Under conditions in the eastern United States the larvae were found to pupate on the plants as well as on the ground (201). The pupal period usually lasts from 10 to 14 days (110, 169, 240, 249, 251).

As the newly-emerged females require a maturation period before they produce eggs, many workers feel that only a small percentage of adults produce fertile eggs during the season in which they leave their cocoons (112, 166, 169, 189, 190).

The climatic limitations to the spread and abundance of the weevils has been for years a classical example of applied ecology. Cook (39) after a study of literature on the biology of the weevil and the climatic conditions of its original home postulated a series of optima and limiting conditions for its increase and spread. The optima conditions are listed as: "(1) a mean annual

temperature of 50°F. or above, (2) summer rainfall not over 4 inches, (3) no winter temperatures below 0°F. or if below in combination with heavy snowfall, and (4) a growing season of 150 days or more." The limiting conditions were listed as: "(1) mean annual temperature below 40°F., (2) summer rainfall over 6 inches, (3) subzero winter temperatures combined with light snowfall, and (4) growing season less than 100 days." On the basis of these data, Cook predicted the weevil to be limited on the north, inside the Pacific and sub-Pacific rainfall regions, by low temperatures, on the east, by heavy summer rainfall and on the northeast, in the plains of Montana and Wyoming by summer rainfall and by low winter temperatures plus a very light snowfall. No data were given to predict a southern limit but he felt that possibly the high temperatures in Arizona and southern California might prove fatal to the larvae. He ruled out the possible change in adaptability of the alfalfa weevil to a new climate by stating that the weevil is a native of Europe and has been limited on the north by purely climatic factors for a very long time and that it "seems probable that it has reached its limit of adaptability by the present time so that little or no further adaptation to cold and moisture will take place." Michelbacher & Leighly (167) in a similar paper to that of Cook, but dealing largely with the southern limit of dispersal, studied the possible spread of the weevil in California on the basis of temperature alone, ignoring precipitation. Basing their work on the climatological data from the insects' native habitat, coupling it with that of Cook and supporting it with temperature optima and limitations as presented in the works of Sweetman (241) Sweetman & Wedemeyer (242) and Yakhontov (285) they predicted a limited spread of the weevil in California. In view of the appearance of the weevil in eastern United States and its rapid spread though ten eastern states, where in many of them it is a major pest, a complete reexamination should be made of its biology, both in the East and the West.

In its native home, there are a number of natural factors which attack the weevil. The most important of these are insect predators, parasites and fungi which attack the different stages of the weevil. A good discussion and bibliography of these natural enemies are presented in Essig & Michelbacher (63) and in the works of Chamberlin (29, 30, 31).

The most important parasite of the alfalfa weevil in the United States is *Bathyplectes curculionis* (Thomson) (112) which was introduced into Utah from Europe in 1911 and by 1919 had spread naturally into Idaho. Parasitism in the field ranged from 2 to 97.3 per cent [Chamberlin (29)]. All instars are attacked, but the percentage of parasitism is greatest among the fourth instar (112) where it frequently reached 100 per cent in May and June. Parasitism by *Bathyplectes* was found to be ineffective during the second-crop period. Other parasites of the alfalfa weevil here or in Europe include *Bathyplectes tristis* (Gravenhorst), found in southern Europe [Chamberlin (31)], and *Hemiteles graculus* (Gravenhorst), found in consider-

able numbers in Italy (31). *Bathyplectes corvina* (Thomson) was recorded by Chamberlin (30) as the most promising parasite of the weevil in southern Europe, especially France, in 1922 and 1923, and by other writers as being present in Sweden, Germany, and Russia.

Several entomogenous fungi have been reported as particularly destructive to alfalfa weevils. The most important is *Entomophthora sphaerosperma* Fresen which is credited with killing 38 to 45 per cent of the weevils in some localities in Utah in 1911 [Webster (271)]. Rockwood (212) found that *Beauveria globulifera* (Spegazzini) Picard killed many of the hibernating weevils. Milliron & MacCreary (169) reported heavy mortality of adults from this fungus in Delaware in 1953 and found it 100 per cent effective in the laboratory but in 1954 found it to be relatively unimportant.

Many species of birds as well as toads, snakes, frogs and shrews have been observed feeding on the alfalfa weevil (144, 271).

Good farming practices which help maintain vigorous stands of alfalfa retard development of the alfalfa weevil and reduce weevil damage (112). Cultural practices such as destruction of overwintering places, harrowing in the spring, dragging or dust mulching, sweeping, burning, irrigating, timely cutting and pasturing have been advocated at times as supplemental controls (112, 190, 206, 249, 251, 258, 271).

Insecticides have long been advocated for weevil control when the larvae are causing serious injury. Zinc arsenite, lead arsenate, and calcium arsenate plus sulfur were recommended by early entomologists (110, 206, 233, 251) followed in recent years by DDT (151). However, all of these insecticides presented toxicity or residue problems.

Hastings & Pepper (118, 119) found that dieldrin applied at the rate of 4 oz. per acre either with ground or air application gave outstanding control of the alfalfa weevil. Such applications were particularly effective when applied to the old stubble in early spring before the new growth was two inches tall and before the overwintering females had laid their eggs. Heptachlor at a similar dosage and chlordane at 1 to $1\frac{1}{2}$ lb. per acre applied in a similar manner have also been found very effective. Other treatments suggested for summer treatment of larvae in the West include methoxychlor, parathion, aldrin, lindane and heptachlor (9).

Under eastern conditions, App (12) found dieldrin to be the most effective insecticide for alfalfa weevil control followed by heptachlor, methoxychlor, endrin and toxaphene in that order. Muka (173) working in Virginia with granulated formulations of aldrin, dieldrin, parathion, lindane and heptachlor found the latter to be most effective when applied at the rate of $1\frac{1}{2}$ pounds per acre either in the winter or early spring.

In general, eastern workers agree that western control measures directed against the alfalfa weevil do not apply in the East where many of the insects overwinter in the egg stage. Under eastern conditions, heptachlor is being generally recommended at 4 to 8 oz. per acre. This is applied at the 6 to 10

in. of growth and is followed by a second application a week or 10 days later if infestations warrant such an application. If infestations are very heavy the alfalfa is removed in the bud stage and another application is applied to the stubble at double the dosage. If pea aphids are also a problem, 10 ounces of malathion are included with the heptachlor in the first application (94).

Meadow Spittlebug

Spittlebug damage to hay was recognized by such early workers as Baxter (19) and Cram (40). Baxter (19) and Lintner (154) reported that hay yields had been reduced as much as one-third by their damage. Surprisingly, little attention was given to this matter, although for centuries laymen and scientists were interested in the froth and—after they at long last associated the froth with the cause—in the insect itself.

The meadow spittlebug, *Philaenus leucophthalmus* (Linnaeus), is common throughout eastern North America and Europe and has been reported from Asia, Africa and South America. Its exact distribution is difficult to determine because of the confusion as to its taxonomic position. It is referred to as *Cicada spumaria* Linnaeus in European literature. A large number of varietal names of dubious biological significance have been proposed to distinguish the various color patterns in which it may exist. Early, Haupt (120, 121) determined 15 distinctive European varieties and 4 intergrades. In North America, Doering (59) in a highly controversial paper recognizes 8 distinct varieties which are described by Haupt (120) as occurring the Old World. The reader is referred to Weaver & King (269) for a discussion of the taxonomic problem associated with this insect.

Nearly 400 species of plants are attacked by the meadow spittlebug [Weaver & King (269)]. Early in the twentieth century the damage caused to forage crops was "rediscovered" by a number of workers in North America and Europe (20, 24, 26, 66, 83, 215, 216, 131, 179). The literature on the spittlebug has since become voluminous; much of its consists of repetitions of previous work, popular articles and extension-type literature (269).

The biology of the meadow spittlebug has been well studied (1, 28, 150, 159, 179, 246, 269). The eggs are laid in masses of 1 to 30 and are held together by a hardened, frothy cement (269). They are inserted between the stem and leaf sheath at a height of 3 to 6 inches above the ground. Straw and other dead plant material are preferred for oviposition.

The eggs hatch from late March (219) to early June (179) from North Carolina (269) to Oregon and Maine. Weaver & King (269) found that the optimum temperature is between 55°F. and 70°F. and that high humidity is important to the successful hatching of the eggs. Medler (161) determined a fairly dependable method of predicting the hatching date of the meadow spittlebug by using an accumulation of day degrees above the daily mean temperature of 40°F. but not exceeding 50°F. He maintains that the eggs will hatch within one week after a total of 150 day degrees is reached. This

information is of utmost importance since applications of even very small amounts of certain insecticides near the time of egg hatch give nearly perfect control with a minimum of residues.

The nymph, which is highly susceptible to desiccation (269) creates its own humid conditions as soon as it begins to feed and excrete spittle. Older nymphs seem to withstand lower humidities better than do younger nymphs. Weaver & King (269) attribute the small populations of nymphs which are found on grasses to the lower humidities which occur there than in mixed legume and grass stands or in weeds. They found larger populations of nymphs on first-harvest year stands of red clover and alfalfa than on older stands which are less dense and thus less humid. Marshall (159) found that older stands of *Lotus* were more heavily infested than young stands. His work thus supports that of Weaver & King (269) since old stands of *Lotus* are usually more rank in growth than first or second year stands.

The populations of nymphs have been measured by a number of ways: nymphs per square foot (283), nymphs per stem, percentage of infested stems (265) spittle masses per unit area or per stem (159) and by net sweeps (65). Chamberlin & Medler (32) tried to resolve the various methods and concluded that counting infested stems is rapid, conservative, and satisfactory. Weaver & Whitney (270) developed a proportion method for sampling spittlebug populations.

The nymph passes through five instars (159, 246, 269) although some workers have reported three (179) and four instars (3). Various workers (28, 159, 269) have reported from 29 to 52 days required for the completion of nymphal development in the field. In cages kept at constant temperatures the period of nymphal development ranged from 31 days at 75°F. to 100 days at 50°F. (269).

Spittlebug adults appear in late May and early June (159, 246, 269) and live until late fall. There is only one generation per year. The adults feed on a wide range of host plants including weeds and cultivated plants. There is some evidence that their feeding can cause wilting and dying of succulent terminals and destruction of legumes in birdsfoot trefoil (176).

With the dissemination of adults from meadows during the summer (269), there is a concurrent increase in croplands, particularly corn, wheat and oats, where they feed as long as the host plants remain tender and succulent. King & Weaver (145) found that movements of adult meadow spittlebugs are conditioned by the availability of succulent foliage and that fall management of meadows determines the attractiveness of legume fields as feeding sites. They found that management practices which promote new growth preceding and during the oviposition period resulted in low spittlebug adult populations and low infestations the following year (145, 269).

As the season progresses the lower temperatures of September and October have a retarding effect on adult migration (269). Weaver (263) found that heavy populations build up in new seedings during late August and early

September and that the majority of eggs are developed at this time. He found these facts useful in determining a method for controlling the amount of egg laying in the fall and the resulting nymphal populations the following spring (262, 266).

Few natural enemies of the adults of the meadow spittlebug are known. Swallows feed on the adults as they fly up in clouds during hay mowing (269). The nematode parasite of grasshoppers, *Agamermis decaudata* Cobb, Steiner, and Christie has been found in adult spittlebugs (269) and Sorauer (234) describes an epizootic of *Entomophthora aphrophorde* Rostr. on *P. spumarius.* Weaver & King (269) describe three genera of egg parasites and indicate that fewer than 10 per cent of the eggs are parasitized.

Some varieties of alfalfa are more resistant to spittlebug attack and others were tolerant to rather heavy infestations of spittlebug nymphs (283). Much work remains to be done in investigating this promising avenue of combatting spittlebug infestations.

The recent revival of interest in the meadow spittlebug has brought a large amount of literature on chemical control. It is difficult to compare the results of such work because of the different methods of application and evaluation and different concentrations and formulations employed by the various investigators. Therefore, the reader is referred to the following papers for detailed discussions on chemical control: (2, 13, 14, 33, 34, 35, 60, 65, 98, 99, 102, 103, 158, 159, 161, 162, 164, 175, 191, 218, 220, 261, 262, 263, 264, 265, 269). In general these workers' results may be summarized as follows: lindane, BHC, endrin and dieldrin at 0.20 to 0.30 lb.; toxaphene at 1.5 lb.; and methoxychlor (as an emulsion) at 1.0 lb. per acre of actual toxicant gave excellent control of spittlebug nymphs. Heptachlor (as an emulsion) and isodrin at 0.25 lb.; DDT (as an emulsion) and chlordane at 1.0 lb. and strobane at 1.5 lb. per acre gave good control of the nymphs, while rotenone, TDE, aldrin, and pyrethrum only gave fair to inadequate control.

Marshall & Gyrisco (158) showed that BHC applied as early as 1 week before egg hatch provided good control of the nymphs. Medler (161) attributed such good control to the fact that newly-emerged nymphs move on the soil surface, and toxicity is due to contact and fumigant action. Similar good results were not obtained with granulated dieldrin and heptachlor. Koehler & Gyrisco (147) established the fact that lindane (gamma isomer of BHC) was translocated in the plant and, in a series of experiments which eliminated contact and fumigant action, showed that lindane could kill nymphs of the meadow spittlebug by systemic action. They postulated that lindane was effective in small amounts, even with poor coverage, because of systemic action (146).

Gyrisco *et al.* (102) achieved better control with sprays than with dusts but failed to get good control with thermal aerosols (158). A number of workers have demonstrated that low volume, low pressure sprays are ideal for spittlebug control and are wholly as effective as high gallonage applica-

tions (34, 158, 263). Granulated formulations have proved to be as effective as sprays and, in many instances, are easier to apply (161, 261).

Weaver and his co-workers, determined the seasonal behavior of the meadow spittlebug and its relation to control (263). They found that little reinfestation of meadows occurs if adults are controlled in late August, prior to oviposition. Such treatments therefore control the nymphs the following spring (262, 266). Ohio and New York now recommend DDT for the control of adults in the fall.

Good spittlebug control results in substantial increases in hay (98, 165, 265), but has little effect on the protein and carotenoid content of the hay (268).

Clover Root Borer

One of the most important pests of red clover is the clover root borer, *Hylastinus obscurus* (Marsham). This insect breeds in the roots of herbaceous leguminous plants, primarily red clover. It is of European origin and was first reported in the United States in 1878 (209). Since that date its distribution has been extended throughout many of the important red clover producing areas of the United States and Canada (211).

The early literature contains widely differing opinions as to the amount and seriousness of injury occasioned by the attack of the clover root borer (42, 79, 122, 133, 154, 155, 170, 177, 193, 211, 217, 273, 277). Nearly all of these data are of an observational nature. Unlike all these workers, Newsom (177) was the first worker to devise sound methods for the quantitative determination of the amount of injury caused by the clover root borer to red clover. His work, plus the earlier work of Rockwood (211), constitute the best and contain the most complete references on the clover root borer to date. Newsom (177) found that injury by the clover root borer reduced the number of leaves produced by a plant by 23 per cent, total sugars of the carbohydrate root reserves by as much as 60 per cent, and the shoot-root ratio approximately 30 per cent. Data based on plant counts and root examinations made in first crop[2] year red clover fields indicated that the borer is responsible for the death of about 10 per cent of the plants in the late summer and fall. The data also suggested that the insect is responsible for the death of approximately 40 per cent of the remaining plants entering the winter low in carbohydrate root reserves. In addition to these losses the root borer weakens the roots to such an extent that many are pulled out during haying and cattle grazing or are heaved out by frost.

In addition to the extensive damage caused by its feeding within roots, the clover root borer has been shown under laboratory conditions, capable of acting as a vector of the red clover southern and northern anthracnose pathogens, *Colletotrichum trifolii* Bain and Essary and *Kabatiella caulivora* (Kirch-

[2] The term first crop year refers to the first harvest year, which occurs a year after the seeding year in most areas where red clover is grown.

ner) Karakulin, respectively (200). The borer is also believed to be associated with the spread of several root rots of red clover (69, 95).

The clover root borer overwinters primarily in the adult stage within galleries formed during larval development in red clover roots. When soil temperatures reach approximately 45°F. in early spring the activity and feeding of the borers are resumed in the roots (211). When air temperatures at the surface of the soil range between 55 and 60°F. the borers leave the roots, mate, and migrate on foot to new host plants if air temperatures remain below 65°F. Beetles begin to fly (177, 211) to new first harvest year fields when the air temperature reaches 70°F. Once flight has begun, it continues even at lower temperatures providing soil temperatures have been sufficiently high to induce activity within roots for some time prior to the rise of air temperatures to 70°F. (211).

Upon reaching a suitable red clover plant, the adults burrow into the root. Eggs are laid in the walls of the galleries in niches. Oviposition galleries may reach 30 mm or more in length and contain up to 9 well separated egg niches (211). Schmitt (217) estimated that 4 to 6 eggs were deposited by each female in Germany, and Rockwood (211) about 20; but Newsom (177) found that in New York, females deposited an average of 36 eggs each during one season, and 58 eggs were laid in 2 years. Borers sometimes infest as many as 4 plants during one season (211). Schmitt (217), indicated that eight days were necessary for the completion of the incubation period in Germany, in May. In Oregon, (211) found that the length of the incubation period varied from 32 days in May to 16 days in June; In New York (177) it was 16 days for eggs stored at approximately 65°F.

Little data on the duration of the larval period under controlled conditions have been recorded. Rockwood (211) reported it to range from 32 to 65 days, and concluded that under normal conditions at least 50 days were necessary to complete larval development. Newsom (177) found the larval period for 173 individuals to vary from 40 to 77 days at 65°F., with a mean of 60 days. The available evidence indicates the larva moults from 3 to 5 times.

Pupation occurs within the root in the gallery and requires from 5 to 14 days (177, 211).

Most European workers, with the exception of Schmitt (217), have maintained that this species has two or more generations each year. Del Guercio (46) concluded that there are 3 generations per year in Tuscany. Most American workers agree with Schmitt, in that there is only a single generation each year, or even a single generation extending for more than 1 year (42, 177, 209, 211, 274).

Very few natural enemies of the clover root borer have been found. The soldier beetles, *Cantharis bilineatus* Say (21) and *Chauliognathus pennsylvanicus*, De Geer; a fungus, *Beauveria globulifera* (Spegazzini) Picard; and several species of birds have been reported to attack the root borer (211).

Early attempts at the control of the clover root borer have largely been of a repressive nature such as leaving red clover down for only one crop (211, 272) plowing badly infested fields (79, 211), and adoption of cultural practices promoting healthy, rapidly growing root systems (211).

Satisfactory chemical control of the clover root borer has been attained with DDT, BHC, aldrin, dieldrin, heptachlor, and chlordane applied as dusts at a rate of 0.5 pound per acre (13, 96, 104, 105, 220); however, aldrin, dieldrin, or heptachlor at a rate of 1.0 pound per acre gave more consistently good results (105). Lindane dusts have also been found to give good control (11, 105, 284). Weaver & Haynes (267) found that aldrin or BHC mixed with fertilizer and placed in bands beneath red clover seed gave good control of the borer at much smaller rates than are necessary for control by surface applications. In such plots, second cutting hay yields were increased from 34 to 82 per cent over the untreated check.

Marshall *et al.* (160) reported that BHC dusts were superior to sprays and that a single application made at the peak of the spring migrational flight was entirely as effective as 2 or 3 applications, and resulted in much lower foliage residues. Gyrisco *et al.* (105) and Woodside & Turner (284) found that good borer control could be obtained by either fall, winter, or spring treatments, although properly timed spring treatments were more generally satisfactory.

Gyrisco & Marshall (104) found no varietal differences in control, in a study of 20 different red clover varieties and seed sources. Some varieties, however, appeared to show some resistance to borer infestation.

Other Forage Insects

This paper would not be complete without at least listing some of the other more important insect problems of grasses and legumes of meadows and pastures. Such arthropods as the velvet bean caterpillar, *Anticarsia gematilis* Hübner; the sorghum midge, *Contarinia sorghicola* (Coquillet); the meadow plant bug, *Leptopterna dolabratus* (Linnaeus); *Lygus* spp.; the southern green stink bug, *Nezara viridula* (Linnaeus); the three-cornered alfalfa hopper, *Spissistilus festinus* (Say); the green cloverworm, *Plathypena scabra* (Fabricius); the vetch bruchid, *Bruchus brachialis* Fahraeus; spider mites; the clover leafhopper, *Aceratagallia sanguinolenta* (Provancher); the clover leaf weevil, *Hypera punctata* (Fabricius); the lesser clover leaf weevil, *Hypera nigrirostris* (Fabricius); the clover head weevil, *Hypera meles* (Fabricius); the clover seed weevils, *Tychius* spp. and *Miccotrogus* spp.; the clover root curculios, *Sitona* spp.; the sweetclover weevil, *Sitona cylindricollis* Fahraeus; green June beetle, *Cotinis nitida* (Linnaeus); the clover seed chalcid, *Bruchophagus gibbus* (Boheman); and the European chafer, *Amphimallon majalis* (Razoumowsky) are important forage pest problems throughout different sections of the New World and in fact in many parts of the Old. Many of these arthropods as well as all of those previously discussed are

pests of forage legumes but as the current trend to increase production of high quality grasses continues one can anticipate more interest in the long neglected study of the arthropods of grasses.

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CONTROL OF FOREST INSECTS[1,2]

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In applied biology empiricism has preceded fundamental study. Only after the limits attainable by direct experiment have been recognized has the nature of a problem been thoroughly investigated to provide a new starting point for empirical attack (1). Thus, although forest insect control is essentially a problem in population dynamics, serious study of the populations involved and the forces that regulate them has only recently been attempted. One result has been that the word "control" has been pre-empted by economic entomologists. It implies a degree of regulation seldom achieved by man and might have been more appropriately reserved for the controlling systems of nature, but usage has forced students of population to avoid it.

The subject of this paper, therefore, is the methods used to protect forests from insect damage. It is too large to permit of more than general treatment and reference can be made to only a fraction of the literature that will help to illustrate the different approaches. Most of the papers are from North America and Europe although much work is being done in the U.S.S.R. (2). The chief problems are in the Northern Hemisphere. This is due to the large areas of forests of relatively simple ecological structure and extremes of climate—conditions which favor instability of populations—as well as the particular vulnerability of conifers.

The literature also reflects the status of forestry. In Europe, with its long history of intensive land use, the forest crop has a high economic and strategic value per acre, there are large areas of planted forest, and protection has been intensive. In the United States, and particularly in Canada, there are huge areas of natural forest, much of which has only recently come under management; forestry practice is less intensive and based largely on natural reproduction. The apparently large reserves of timber have encouraged some complacency about insect losses in the past and methods of control, even salvage, have needed to prove their economic necessity (3). On the other hand, a number of devastating outbreaks have stimulated the interest of government and industry and some large projects have been undertaken (4). The need for fundamental research has also been recognized. In Canada a Division of Forest Biology has been created for long-term study of entomological and pathological problems, including ecological projects integrated with research on silviculture and management (5, 6, 7). A similar trend in the United States Forest Service is indicated by Beal (8).

[1] The survey of the literature pertaining to this review was completed in May, 1957.

[2] Contribution No. 412, Forest Biology Division, Science Service, Department of Agriculture, Ottawa, Canada.

An increasing similarity of approach on the two continents was illustrated by symposia at the Tenth International Congress of Entomology, on the use of aircraft, surveys, biological control, and population studies in forest insect work. Differences remain, however, in the nature and scale of problems, as indicated in Schwerdtfeger's (9) account of his impressions of Canada, "Land of the Superlative." In Europe the chief problems are in artificial monocultures and natural mixed forests have been considered resistant. The most devastating outbreaks in the world have occurred, however, in natural forests of North America, which few European foresters would call "pure." At the same time the relative resistance of mixtures of tree species is also recognized in America (10, 11).

The literature from Africa and Australasia is more limited but suggests that forest insect control is increasing in importance as plantings of exotics mature (12, 13). If the following discussion refers chiefly to North America it is partly due to the author's greater familiarity with work on this continent, partly to the extent of its problems.

Several comprehensive works have been published in recent years. Craighead edited a valuable book describing the forest insects of the eastern United States and known methods of control (14). Keen's similar publication for the western states was revised (15). Graham's well-known work on the principles of forest entomology, emphasizing the ecological viewpoint, was brought up to date (16). Gäbler has presented a systematic treatment of the animals harmful to Central European forests with control measures for many insects (17). A revision of Schwerdtfeger's valuable discussion of the causes of injury to forests, with an extensive summary of control measures, will be published in 1957 (18). Much information on the ecology and control of forest insects of northern Europe is provided by Saalas (19). The German literature from 1943 to 1954 has been concisely reviewed by Thalenhorst (20).

Among the papers indicating the status of control and research are Prebble's (21) discussion of work in Canada, Beal's (8) summary for the U.S.A. and a report on forest protection in the U.S.S.R. (2).

General Principles

Forestry differs from agriculture in the greater time necessary for the crop to mature and the lower annual financial yield per acre. Protective measures must be correspondingly low in cost and lasting in effect. They must also be applied with due regard for the complexity of the ecosystems involved. The forest entomologist is particularly conscious of the dynamic nature of the populations he seeks to control. He has always been less able and more reluctant to use direct methods, although a growing number of agricultural entomologists emphasize the ecological approach (22). The new insecticides and aerial methods of application, however, have increased the use of chemical control (23, 24, 25). Thus the interests of agricultural and forest entomologists seem to be converging (26). At the same time the limitations of DDT and its successors have become apparent and have stimulated

research on their effects on the complex of factors that determine insect abundance, particularly in the case of perennial host plants, of which forest and orchard trees are prime examples (21, 24, 27, 28, 29).

Control may take the form of prevention or cure, hygiene or therapy. Schimitschek has discussed the organization (29) and fundamentals (30, 31) of hygiene, which he describes as the promotion of the self-regulation of the forest community. He attributes outbreaks to the replacement of natural forests by monocultures and other unstable communities. His historical, and somewhat philosophical, approach may be compared with Thalenhorst's (32) review of recent literature. While stressing the value of prevention he points out that the merits of hygienic, as well as therapeutic, methods must be determined by critical study rather than speculation or claims based on accidental successes and prejudice. He makes the interesting remark that "Anglo-Americans," who cannot be accused of "sentimentality," spend considerable sums on such research.

Prevention is better than cure and the ideal solution is the creation of resistant forests. In such a forest all the factors that regulate insect numbers must be so combined that the crop can be grown, harvested, and reproduced without disturbing them. Some of the principles will be discussed below, but the completely resistant forest will remain an ideal until much more is known about the causes of outbreaks and the application of this knowledge is translated into practical silviculture. Meanwhile, the control of forest insects must be sought in appropriate combinations of therapy and hygiene (5, 6, 10).

Methods are classified on the basis of techniques as chemical, biological, and silvicultural. The term "biological control" has been used by some authors to cover silvicultural methods but common usage suggests that it be reserved for the manipulation of parasites, predators, and diseases (33).

Chemical

Insecticides.—The continually growing number of highly toxic organic insecticides has led to considerable dependence on chemical control in agriculture. This has been less marked in forestry but there are few forest insects for which effective poisons are not now available. Zwölfer (34) warns against relying on them to the neglect of other methods—a decision that may become irrevocable.

DDT is still most commonly used. Because of its toxicity and low cost it is the basis of all large-scale spraying operations in America (24, 35). Butovitsch (23) has reviewed its many uses in Europe. All species are sensitive in varying degree but it is particularly effective against free-living defoliators and has been used extensively against such notorious pests as the nun moth, *Lymantria monacha* Linnaeus; the gypsy moth, *Porthetria dispar* (Linnaeus); and the spruce budworm, *Choristoneura fumiferana* (Clements). In these cases its chief effect is as a contact poison but this is reinforced by "stomach" and "residual" poisoning. Its prolonged residual toxicity can be used against certain species to prevent oviposition, or to kill larvae emerging from the egg

or crawling over sprayed surfaces, and beetles entering or emerging from bark.

Barkbeetles of the genus *Dendroctonus* have been perennially destructive in America and outbreaks of *Ips typographus* Linnaeus followed the neglect of European forests during the war. The trend has been away from direct control in the United States (36) but standing or felled trees are sprayed with DDT in oil, orthodichlorobenzene, or ethylene dibromide (37). In Europe felling and peeling has been supplemented by spraying infested trees, the ground beneath them, or trap logs (38, 39, 40). The barkbeetle vectors of Dutch elm disease are controlled in America by spraying infested or susceptible trees but in England Peace considers the cost prohibitive (41).

Damage by borers and ambrosia beetles is normally prevented by winter felling, debarking or prompt salvage but logs may be sprayed with DDT, BHC, or ethylene dibromide when necessary (8, 42). In a review of work on ambrosia beetles Fisher *et al.* (43) advise research on biology rather than insecticides.

Planting of white pine has been abandoned in America because of "crooking" by the weevil, *Pissodes strobi* (Peck). Belyea & Sullivan (44) review the problem, suggesting how intensive biological and silvical studies may lead to restoration of this valuable tree to production by cultural control. Meanwhile plantations may be protected by aerial spraying with DDT. This may be necessary only every three or four years until the trees reach 25 ft. (45). Attempts to avoid the problem by planting red pine were frustrated by attacks of the European pine shoot moth, *Rhyacionia buoliana* (Schiffner), for which spraying is also necessary (46).

Chemical control of species of *Melolontha* and *Hylobius*, the chief enemies of young plantings, is almost standard practice in Germany. DDT and BHC are applied singly or together to the roots or soil at planting (47 to 50). When plantings are large in relation to surrounding deciduous stands, spraying the latter to kill adults is preferred (51). Dipping seedlings in DDT may protect them for over a year, does not affect the biocoenosis, and is claimed to promote growth (52). In the U.S.A. damage by *Hylobius* is usually avoided by delaying planting after cutting, but insecticides are being tested (54). In the U.S.S.R. treatment of planting stock with BHC or the "sterilization" of soil every four to five years is recommended (2).

Residual effects of DDT can be used against species whose wingless adults crawl up trunks to oviposit (55). Spraying the lower part of the trunk may be less effective than foliage spraying but only simple equipment is needed and parasites are not killed.

Systemic insecticides deserve more attention. Complete mortality of a thrips and a needle-mining caterpillar has been obtained by Vité and others (56, 57, 58) by ringing larch with an absorbent soaked in demeton, without injuring the tree. Poisons of this type may be applied more cheaply by spraying (59) and have given good results against *Dreyfusia nüsslini* Börner (60). Quassia extract applied to the soil of potted evergreen and deciduous trees

will kill aphids, sawflies, and caterpillars (61). Several systemics are rapidly transported from roots to foliage and give persistent toxicity (62). Internal insecticides will directly affect only species feeding on the tree—a desirable form of selectivity.

The need for more selective poisons, nontoxic to beneficial insects and wildlife, is apparent (24). As yet there has not been sufficient evidence of the detrimental effects of DDT to discourage its use against forest insects. Few species have been exposed for many generations and the phenomenon of resistance has not been encountered. Although its use on ornamentals has sometimes encouraged mites, aphids, and scales, no outbreaks have yet resulted in the forest. However, the possibilities of the newer insecticides, such as the organic phosphates, offer a promising field of research.

Techniques.—Roughness of terrain, impenetrability of stands, and height of trees often prevent treatment from the ground. Developments in the use of aircraft have been reviewed by Balch, Webb & Fettes (24), and by Johnson (25). There have been considerable advances in techniques since the war and a number of large operations have been undertaken, particularly against the spruce budworm. Over 20 million acres have been sprayed in Canada and the U.S.A. since 1949 (63). Numerous projects have been carried out in other countries against various defoliators (23).

Spraying large areas calls for careful organization if adequate coverage is to be obtained at the right time. Fleets of up to 200 aircraft have been used, with many specially constructed airstrips linked by wireless communication. Pilots fly from aerial photographs, sometimes in teams, and are checked by aerial inspection. Coverage is aided by spray drift, which gives wide overlapping effective swaths. The spraying equipment is a boom, with nozzles adjustable for calibration. Efficiency is largely dependent on drop size (64, 65), the optimum being the smallest size that will reach the trees before evaporation. There is need for improvements in equipment that will reduce the size range.

Timing may be vital. Not only must the poison be applied when the insect is most vulnerable, but also when it will give the maximum protection to the trees. This is illustrated by Webb's attempt to reconcile the two objectives by estimating the optimum time and the range within which different degrees of success may be expected (66). Another question is the stage during an outbreak when spraying should start: Can it be checked in early stages, or should spraying be delayed until necessary to prevent serious damage? The latter has been the policy with the budworm, on the grounds that it avoids unnecessary spraying and obtains the maximum control from natural factors. Also outbreaks develop over large areas and the recognition of foci of infestation is difficult. Uncertainty about ultimate effects on population trend suggests the prudence of limiting the objective to preventing tree-killing defoliation rather than attempting to control outbreaks. More information is needed.

Good survey techniques are necessary to planning and assessment. They must be based on intensive study of seasonal history, natural control, popu-

lation trends, and relations between population and damage. Extensive methods of sampling and surveying from the ground and the air can then be worked out (24, 25, 67).

Aerial spraying with 1 pound DDT in 1 gallon of oil per acre is almost standard practice in the U.S.A. It is used annually against the gypsy moth in what has been referred to as a program of "eradication" (35)—an example of optimism unsupported by the literature. Research on techniques is being continued (68). In Canada the dose has been halved by doubling the distance between flight lines, and two applications are made when necessary. This tends to check defoliation more rapidly and improve coverage (24). Techniques in other countries have been varied and spraying has replaced dusting more slowly (23, 69, 70). Helicopters are too costly and light conventional aircraft are generally preferred (24, 71).

For ground spraying "mist blowers" have replaced "solid-stream" sprayers. Concentrated formulations are used, with corresponding reduction in volume, and even oil solutions are applied without injury to foliage. Heights of over 100 ft. can be reached. Potts, who has played a leading part in this development, recently described a "dual nozzle" system, which uses larger droplets for height (72). Fogging machines are employed extensively in Europe (73).

Assessment.—The immediate results may be assessed if comparable treated and untreated areas can be adequately sampled. The method must separate mortality due to treatment from that which would have occurred without it, and "check areas" are essential (24). The problem is to measure the effects of introducing a new factor into a complex already causing high mortality. Solomon (74) suggests assessment in terms of the time required for the population to regain its original density. Morris (75) has shown clearly the importance of correct interpretation of mortality data. Owing to the interrelated variability of factors no one factor can be considered alone. Also the value of minor differences in percentages increases with the level of total mortality. The simple percentage killed by an insecticide may indicate the immediate protection given the trees, if the population level is known, but is no indication of its effect on population trend.

The importance of effects on density-related factors is evident. The insecticide may only anticipate mortality that would otherwise result from lack of food or dispersal; it may even cause a higher rate of survival. For these reasons control of the treated generation is often calculated from the number of adult survivors. Webb has used the method of sampling pupal cases after emergence (63). In developing life tables Morris & Miller (76) expressed mortality from DDT as a percentage of the larvae killed but pointed out it would have been twice as large if based on surviving pupae. While percentages based on surviving populations are not suited to comparisons of the effectiveness of factors from year to year they do express concisely the end result of a control operation as far as the current generation is concerned.

Assessment of ultimate results calls for comparative studies of population

trends and control factors until after the outbreak subsides (24). The need is recognized but information on events following the year of treatment is fragmentary. Thalenhorst (77) and Kolubajiv & Kalandra (78) state that outbreaks of *Lygaeonematus abietinum* Christ continued unchecked the year after 80 to 96 per cent of the larvae had been poisoned. This was attributed to killing of parasites and to the number of larvae in diapause (23). Summaries of operations against the spruce budworm in the U.S.A. show the progress of the outbreak from 1944 to 1956 and the areas treated from 1949 to 1955. It is concluded that the decline of the outbreak and limited mortality of trees was associated with the spraying. There were no adverse effects on the biocoenosis and parasitism apparently increased (79).

Studies of the biological effects of the spruce budworm project in Canada are in progress (63). It presents perhaps the most severe test of chemical control that has yet been made, owing to the "aggressiveness" of the insect and the huge areas of forest favorable to its multiplication. The results will not be known until the outbreak subsides, but the following information has been obtained.

(*a*) With good timing and coverage the population can be reduced as much as 99 per cent. Reinfestation has been rapid, however, owing to mass flights of adults from considerable distances and increase in residual population. The latter has been greater than in unsprayed areas, but this is not due to reduction in parasitism.

(*b*) Defoliation has been reduced and good recovery of tree growth occurred the year following. Unless spraying was repeated defoliation generally became severe again in the second year.

(*c*) Best results were from a double application of ½ lb. DDT in ½ gallon of oil per acre. Spraying every year has given excellent protection. The trees can be kept alive for a considerable time by spraying every other year, commencing after two to three years of heavy infestation. This increases the opportunity for salvage and, unless the outbreak is prolonged, should prevent mortality.

(*d*) The general effect on the local budworm population to date has been to check its decline through starvation, by keeping trees alive. Aquatic insects, and some terrestrial species, have been temporarily much reduced. There are no signs of destructive species being encouraged or adverse effects on birds or mammals. Young salmon are killed and the effects on mature salmon population are being studied (80).

The potentialities of chemical methods and their proper place in forest insect control can only be determined by operations on a sufficient scale to achieve their purpose. Even large-scale experiments can provide inconclusive results if not continued long enough to give the required protection (81). The above project should add to our knowledge of the possibilities of preventing damage by species capable of severe, prolonged attack over thousands of square miles. It seems likely to indicate that this can be done if fairly large, continuous areas are treated. They should be restricted to forests

where the necessity is clear, and the values are such that the expense of a thorough operation is justified. Chemical control should be used in the context of a sound management plan.

Careful studies of total biological effects are essential. The method should not be discarded without trial, on the grounds of theoretical dangers or unfounded generalizations about "natural forests" (82). The task of the forest entomologist is to determine when it is necessary and, by study of the population dynamics involved, to assess results as fully and objectively as may be possible. At the present stage we need data more than theory.

At the same time it should not be used without regard for the effects on the whole biocoenosis (10, 34). If possible it should be timed, or insecticides should be chosen, to minimize the damage to natural enemies (23, 83, 84, 85). To date, reliance has been placed chiefly in limiting the dose or number of applications.

Biological

"Biological control" is used here in referring to methods involving the direct manipulation of "natural enemies," including pathogenic microorganisms, by introduction or propagation. It is essentially a form of therapy although the eventual results may be considered as hygienic. It does not include indirect measures for improving natural control, which are largely silvicultural although they may favor the action of natural enemies. Reference is made, however, to the encouragement of nonspecialized predators such as birds and ants, which Thalenhorst (32) considers as an aspect of hygiene.

Biological control has been employed most extensively in North America. A total of 485 species of parasites and predators have been imported to the U.S.A. against 91 insects, of which 10 are forest pests (86). In recent years biological control of forest insects has received considerable attention in Canada. One reason is the number of major pests that have been introduced from Europe. As the movement of pests in the reverse direction has been less frequent, or forest conditions have been less favorable to their multiplication in Europe, interest in biological control on that continent is more recent (87, 88). On the other hand much work has been done on native birds and ants in Germany (89).

The value of biological control has been discussed in recent papers. In 1951 Clausen (90) concluded that "full commercial control" had been achieved in only a limited number of cases by introduced entomophagous insects, and that they would show this ability at points of colonization within three years or less. Thompson (91) presented a theoretical basis for the latter hypothesis. Sellars (92) pointed out that there may be a time lag depending on the effect of rate of dispersal on attainment of "equilibrium of distribution," and stressed the fact that the value of a parasite or predator is not constant.

Taylor (93) claimed that most of the cases where biological control could

be effective have already been dealt with. He seemed to think that it is only successful when it makes other methods entirely unnecessary. Simmonds (94) took exception to his limited definition of biological control and his failure to recognize the value of partial control. More recently Clausen (86) has expressed the view that most biological control projects may be expected to yield results of partial value.

Some of the criticism of biological control has been due to the limited information on results. The sceptic has had little difficulty in finding cases where success has been implied but proof is lacking. The difficulties of obtaining convincing evidence of the value of a single factor were discussed by Balch & Bird (95) in presenting data on the control value of a virus disease—a relatively simple case in which the virus caused over 99 per cent mortality. Continuation of the study for 20 years has shown the variability of disease and parasites as control factors at different levels of population (96). Doubts regarding biological control have generally been based, however, on the assumptions that it must be sufficiently effective to make other methods unnecessary, that this is unlikely except in geological or ecological islands, and that a tropical, or an equable, climate is necessary (93). These ideas receive little support in forest entomology.

The level at which forest insects must be controlled is generally higher than with agricultural insects. Most deciduous trees, for instance, will survive total defoliation for two or more years and the loss of growth may not be sufficient to warrant costs of protection. Coniferous trees will usually be killed by complete defoliation but most of their defoliators do not strip the trees until after several years of heavy infestation. Unless outbreaks of bark-beetles or borers are initiated some loss of growth and death of the weaker, less valuable trees may be tolerated. Continuous control at low levels is most necessary with species that injure the form of trees. In many cases it is only essential that the length or intensity of outbreaks be reduced, and partial control by biological methods will suffice.

The possible value, as well as the limitations of biological control, may be illustrated by the balsam woolly aphid, *Adelges piceae* (Ratzeburg), in Canada (97). Chemical control is impracticable and control by management will take time and will not eliminate the damage. A number of predators have been introduced. One has become established throughout most of the infested region but is dependent on rather dense populations and has not prevented the killing of trees. There is good evidence, however, that it has decreased the severity of infestations and reduced the rate of dispersal. Another has been established more recently and shows ability to check infestations before trees are killed by "stem attack." The rate of damage and spread has been reduced but much more effective control is needed. Predators that will attack the aphid at lower densities are being sought.

The assumption that insular conditions are necessary to success has no clear foundation (94). Tooke (98) gives an example of good results with an introduced parasite under continental conditions; the parasite "gradually

assumed control, season by season" and its effectiveness varied in different climatic regions. The European spruce sawfly, *Diprion hercyniae* (Hartig), illustrates the possibilities of biological methods in continental areas and the value of a varying complex of factors. An outbreak developed in the 1920's and spread over some thousands of square miles, gradually killing large quantities of spruce. No parasites or disease attacked it, and a number of parasites were introduced in the 1930's. One of these, *Dahlbominus fuscipennis* (Zetterstedt), was artificially propagated, became widely established, and began to kill considerable percentages of the sawfly. Others that were liberated in small numbers, became established locally and at least one, a species of *Exenterus*, was causing significant reduction in larval numbers at the point of liberation within two years (99). Study of the ultimate value of the parasites was interrupted, however, by a virus epizootic which destroyed such a high proportion of the larvae that other factors became insignificant (95). The origin of the virus is unknown but the evidence suggests it was introduced with the parasites. Since the end of the outbreak the sawfly has remained at relatively low levels. The virus is still present, killing only small numbers but in a proportion that tends to increase with the population. The species of parasites that were most effective during the outbreak have become scarce or disappeared and have been replaced by other introduced species which are now major mortality factors. Methods of propagating and storing the virus have been developed and it has been introduced to areas where it did not occur.

In this case the most spectacular agent of control, a virus, was not deliberately introduced but was a fortuitous by-product of work on parasites. Its importance, however, was recognized in the laboratory several years before it became epizootic in the field and the fact that a serious attempt at biological control was being made was responsible for the intensive study that it was given. The knowledge obtained was applied in the control of another introduced sawfly, *Neodiprion sertifer* (Geoffroy). A virus of similar polyhedral type was obtained from Europe, and in 1953 Bird (100) described its successful application to plantations by means of aircraft. The method has also been used in the United States and given "complete control" (101).

There is a growing interest in viruses and other disease organisms. They are being studied in the laboratory, as mortality factors in the field, and from the point of view of their potentialities in biological control (102 to 106). A number of new viruses are being discovered and it appears that they exist in many insect species. Some of them are known to have a wide range of pathogenicity, which the theory of "latency" may help to explain. Study of the existence of latency, its nature and causes, should enlarge the possibilities of using viruses. Another important characteristic of at least some of these viruses is their apparent strong specificity as to host, which makes them selective in their action. Smith (107), however, reports that a pathogenic virus obtained from *Pyraemis cardui* (Linnaeus) has been transmitted to a large number of other species of Lepidoptera, although it is possible that a

complex of viruses is involved. His suggestion that "certain lepidopterous pests not observed to develop virus disease could be given virus from some other unrelated species" is revolutionary. He has kindly supplied some material from his experiments and this is now being tested against several geometrids in Nova Scotia.

The increased attention to diseases is a notable recent development in biological control of forest insects. The assumption that diseases are too dependent on climatic conditions to be of much value is being re-examined. Although they are limited by host resistance, dissemination capacity, and climatic checks, there is little doubt that other cases will be found in which they can be used to prevent or control outbreaks.

In general biological methods aim at permanent results and tend to be self-perpetuating. At the same time they vary considerably in their effectiveness both in place and time. A parasite or predator may have a narrower range of tolerance to climatic factors than its host and be effective only where or when these factors are favorable. Its effectiveness may vary owing to its dependence on host density or on an alternate host (97). The demonstration of control value may be delayed by rapid dispersal or by liberation at a time when ecological conditions are temporarily unfavorable (92). Conversely, high parasitism or predation may follow rapidly on liberation but for various ecological reasons may not be maintained. The variability of the environment in its effects on both the pest and its enemies prevents their relations from remaining constant. Also the host may develop resistance. Muldrew (108) showed that the larch sawfly, *Pristiphora erichsonii* (Hartig), has become resistant to the previously effective parasite, *Mesoleius tenthredinis* Morley. The development of resistance to parasites and microorganisms is probably a common phenomenon although this seems to be the first recorded case with a parasite.

Dowden (109) indicated some of the limitations of parasites in a review of biological control of forest insects in the United States up to 1948. He noted that there had been few spectacular successes but the method is particularly suited to forest insects. The most extensive work was against the gypsy moth. Although severe outbreaks still occur regularly the introduction of parasites is considered to have brought the insect under a degree of control equal to that in Europe. Its abundance is related to forest site and composition (110) and it is difficult to separate the direct effects of the environment from its indirect effects through its influence on parasites. The interesting relations between biological, chemical, and silvicultural control do not seem to have yet been clearly worked out.

One other example of limited but apparently valuable results from parasite introductions may be given. Several species were imported from Europe to the United States against the satin moth, *Stilpnotia salicis* (Linnaeus), between 1927 and 1934. Of these, *Apanteles solitarius* (Ratzeburg) and *Meteorus versicolor* (Wesmael) became established and have parasitized as much as "60 per cent or more" of the pest (86). At the same time *Compsilura*

concinnata (Meigen), which was introduced against the gypsy moth, has attacked the satin moth and often caused equally high parasitism. The decline of infestations in New England is attributed to these parasites. As the moth spread into Canada they followed it and high parasitism by *A. solitarius* and *C. concinnata* has been recorded (111). The former has reached Newfoundland over some 100 miles of sea, probably carried in the air within the young larva of its host, a remarkable illustration of dispersive capacity of both host and parasite.

The evidence is largely circumstantial but suggests the following principles:

(*a*) In order to discover all indigenous mortality factors, introductions should be preceded by thorough study in the areas where they are to be made so that it may be possible to estimate the subsequent effects of adding to them. This may also indicate the weaknesses in the control complex that need correction, such as lack of parasites or predators (99), and the stage on which attack would be most effective (28).

(*b*) The search for additional factors should be directed preferably to areas where the pest, or a closely related species, exists under similar ecological and climatic conditions but at lower population levels. This will increase the chance of obtaining species that will survive and be effective in the area of introduction.

(*c*) Ecological studies should be made of the host and its natural enemies in the area of search. The prime object should be to discover which parasites are strictly primary, which predators are specific to the pest or its relatives, and whether pathogenic microorganisms are present. Such studies will indicate the factors that can be safely introduced and which are most likely to warrant the cost. The ultimate value of a species can be discovered, however, only by actual introduction. The species which are most successful in the area of origin will not necessarily be most successful in the area of introduction.

(*d*) The larger the number of factors introduced the greater the chance of success. Competition between them should not reduce total effectiveness. A number of species, occupying different niches and with different ecological requirements, is most likely to maintain control under varying environmental conditions (97).

(*e*) Results must be evaluated by quantitative ecological studies of the host and its control complex, commenced before introductions and continued at least until the introduced factors have reached "equilibrium of distribution" (13, 92, 98). Franz (87) has indicated the difficulties of such work and some experimental methods that may be used. The most reliable method will be to study natural populations before and after introductions, or in comparable areas with and without the factors concerned. This involves the construction of life tables which will show not only the mortality caused by each factor but how this has affected population trends (76). In this connection Miller's method of measuring parasitism is of interest (112). Measurement of

predation when the predator leaves no identifiable remains presents one of the numerous difficulties (87) but until a number of such studies have been completed biological control will remain on an empirical basis. We need to know more about the characteristics essential to success, such as searching ability, dispersive capacity, "appetite," and synchronization of generations (97).

(*f*) Biological control must be co-ordinated with other methods. It may be advisable to restrict or delay chemical operations at the risk of some loss of trees (113). Life table studies should serve to indicate the ecological conditions under which biological control may be relied on, alone or in combination with silvicultural methods, and those under which chemical control is necessary. The object is to reduce the latter to a minimum.

Mention should be made of work on small mammals, birds, and ants although they have not been used in biological control as defined above.

Among the small mammals shrews are of particular importance in North America. They are numerous in most forest types, have large appetites, and often destroy large numbers of sawflies that pupate in the forest floor (114). None occur on the island of Newfoundland and the desirability of introducing them is being investigated. As insectivores they appear to be strictly beneficial.

In Europe attention has been drawn to the value of bats. Owing to nocturnal habits and high consumption of harmful moths they complement predation by birds (32, 115). Issel (115) recommends their establishment and encouragement by means of concrete shelters, a proposal supported by Krzanowski (116).

The protection and encouragement of birds has been extensively practiced in Germany. Much detail is given in a comprehensive book by Henze (117). Pfeiffer & Ruppert (118) report that under favorable conditions breeding populations may be increased to as many as 60 pairs per hectare by providing various types of nests and watering. Thalenhorst (32) reviewed the literature and pointed out some of the limitations and technical prerequisites. Bruns (119) also stressed the need for unbiased long-term research to determine the qualitative and quantitative limitations of bird management. He pointed out that the control value varies with species and population densities, and the maximum density of birds is not the optimum. He recognized their hygienic importance but considered that intensive measures should be limited to areas where insect hazard is high. In Czechoslovakia Fric (120) urged that more use be made of nesting boxes.

Most authors believe that birds play a part in the control of certain types of forest insects at low densities, and that they tend to retard if not prevent outbreaks (121). Their feeding habits and territorial relationships, however, prevent them from responding in any marked degree to increases in insect numbers and they become ineffective during outbreaks (122). Since Tinbergen's work (123) the need for careful studies of food selection and relation to insect density has been apparent. In general bird management is con-

sidered a part of forest hygiene rather than a method of biological control. It has received little attention in America apart from protection from shooting. In natural forests birds are seldom limited by availability of nesting sites.

The use of the red ant, *Formica rufa* Linnaeus, as a means of combatting forest insects has been promoted by Gösswald, whose work has been brought together in a book (124). Wellenstein (125) has examined its effects more critically and Thalenhorst (32) has reviewed the considerable literature. The evidence suggests that the establishment and protection of ant nests reduces populations of caterpillars and sawflies within about 40 meters of the nest, but during outbreaks the ants have little effect. It appears to be another case of probably hygienic value under certain conditions but proof that this can be profitably increased by artificial means is limited.

In brief, the literature suggests many possibilities in biological control but emphasizes the need for study of the exact effects on population dynamics. That results will often be limited, and sometimes negligible, is inherent in the method. It should not discourage the testing of all agents of control that offer promise, provided they can be studied. That the work should be carried out with due regard for the competing claims or possible interference of chemical or other methods is axiomatic, but this problem does not seem to have been a serious one in forest entomology.

Silvicultural

Silvicultural control embraces modifications of the methods of growing or harvesting the forest crop that are designed to reduce insect damage. It is almost synonymous with forest hygiene since it includes practically all the known methods of prevention other than those noted under biological control. It is convenient to include also methods of forest management that are not strictly silvicultural, such as salvage or "presalvage" cutting, or ways of handling logs to prevent borer attack (11, 16).

In discussing the fundamentals of forest hygiene, Schimitschek (30) lists 14 causes of forest susceptibility to insects and diseases, all of which except dust, smoke, and water pollution may be considered as silvicultural errors. They boil down to the growing of trees under physiologically unfavorable conditions, or the creation of stand conditions unfavorable to natural enemies of pests. He equates the healthy with the "natural" forest. Among the practices to be avoided are monocultures, "unnatural" mixtures, planting of species on unsuitable sites or outside their optimum range, large-scale clear-cutting, destruction of litter, and impoverishment of the beneficial insect fauna by removing the plants on which their secondary hosts depend. His conclusions are supported by numerous examples.

European entomologists have frequently drawn attention to the high susceptibility of artificial forests. The prevalence in Europe of plantations of single species, often outside their natural range, has been associated with severe outbreaks of a number of defoliators and other "primary" tree pests. The comparative scarcity of natural forests in Europe may be partly re-

sponsible for the conclusion that they are more or less immune. The evidence is strong, however, that many pests, including foliage feeders, barkbeetles and sucking insects, have been favored by the planting of pure stands outside their range, or on sites where they do not occur naturally.

The term "natural forest" lacks precision. If it means simply a forest originating from natural regeneration, many "natural forests" of North America are highly susceptible. If it means "climax forest," there is some support for the idea that such forest types tend to be less susceptible than those that represent earlier stages in the succession. Stands of intolerant hardwoods that generally follow fire in Canada are, for example, highly susceptible to the forest tent caterpillar, *Malacosoma disstria* Hübner. Susceptibility to the spruce budworm is closely related to the proportion of balsam fir and this is generally highest in stands following disturbances such as clearcutting or windfall. Graham (10), in discussing the "law of natural compensations" in relation to forest insects, states that outbreaks result when cataclysms simplify community composition and gives examples of the susceptibility of succession types and plantations. If the concept of climax types is valid and they are known for the various sites of a region, they may be a guide in the creation of resistant forests (11). Forestry, however, is concerned with growing wood of economic value rather than preservation of natural types of vegetation, even if these can be shown to be resistant to insects. In his review of the barkbeetle outbreaks in Germany Schwerdtfeger (126) remarks on the "Utopian" demand that spruce be grown only where it occurs naturally.

The problem is to determine those stand characteristics that favor outbreaks, and to what extent and by what methods they can be avoided. No silvicultural system, or set of systems, will provide universal prophylaxis but certain principles emerge from the literature.

(*a*) The "vulnerability" of trees to damage decreases with their vigor, as expressed by rate of growth. In other words, within a given species and age-class, and with a given degree of infestation, the trees that are growing most rapidly have the greatest capacity to recover. Many cases are known and it is doubtful if there are any to the contrary.

(*b*) The extent to which "susceptibility" to infestation decreases with vigor is less clear. There are cases where the opposite is true. The white pine weevil prefers dominant fast-growing trees. The balsam woolly aphid also tends to select larger trees that are growing faster than the rest of the stand (127). Many species, however, are favored by low host vigor. This is most evident with the borers and barkbeetles that breed only in weakened or dying trees except during outbreaks (128). Keen (129) has described vigor classes as a guide to the removal of trees susceptible to *Dendroctonus* spp. The association of unfavorable sites with outbreaks in Europe suggests that low vigor is the cause. Outbreaks of the hemlock looper, *Lambdina fiscellaria* (Guenée), generally arise in slow-growing, mature or overmature stands (130), and the same is true of the spruce budworm, but there is no

proof that this is related to the vigor of the trees; flower production associated with age appears more important with the budworm.

(*c*) Silvicultural practices that maintain vigor of growth decrease "vulnerability" to damage and will also decrease "susceptibility" to infestation by many species. In particular overmaturity, overthinning or underthinning, and planting on unfavorable sites should be avoided.

(*d*) Mixed stands are in general less susceptible than pure stands. This is one of the principles most commonly put forward by authors but it must be interpreted with caution, and in a relative sense. Some insects, like the balsam woolly aphid (127), and many polyphagous species, will thrive in mixed stands. When, however, the favored host is scattered in mixed stands dispersal loss of the pest is high (131). As first suggested by Voûte (132) the richer fauna of mixed stands is less subject to violent fluctuations and this probably also makes them less susceptible to outbreaks.

(*e*) The larger the area of a susceptible forest or stand type the greater the danger from outbreaks. This is probably true of most insects owing to reduction of dispersal loss as has been shown for the spruce budworm (131). Management should avoid large compartments of even age and uniform composition. The closer the approximation to "normal" age-class distribution, whether by selective cutting or by clearcutting in small units, the less the hazard. The creation of this ideal type of forest is far from simple in the case of the budworm owing to the large areas of even-aged, susceptible stands, many of which have originated from past outbreaks. Full use of balsam fir on a short cutting cycle and the development of methods of increasing the proportion of less susceptible species should, however, eventually produce a more resistant forest (11). The planting of large areas of single species, especially exotics, should be avoided (133).

Space prevents mention of many specific recommendations, such as controlling water levels, use of fertilizers, disposal of logs or slash, methods of cutting, and the breeding of resistant trees (134). Although the above principles seem to provide a general basis for the reduction of insect damage, they apply in greatly varying degree to different species. Much combined research in silviculture and pathology, as well as entomology and population dynamics, is needed to test their value (5, 44). Meanwhile it may be concluded that silvicultural practices that favor tree growth will seldom conflict with, and will often coincide with, protection from insects.

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TRANSMISSION OF PLANT VIRUSES BY ARTHROPODS[1]

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Introduction

At the present time over 300 separate plant viruses have been described, but by no means all are known to have insect vectors. Probably some viruses have no vectors but depend on other means of spread such as mechanical contamination and transmission by the soil. Incidentally this last method needs much fuller investigation and many more plant viruses are probably soil-transmitted than is thought to be the case at the moment. Progress in the study of the general methods of spread of plant viruses has undoubtedly been delayed by a too ready and uncritical acceptance of ideas belonging to earlier generations of plant virologists. The axiom was laid down that soil-transmission was very rare and that, with very few exceptions, all insect vectors belonged to the Hemiptera. Added to this was the fixed idea that there were no leafhopper-transmitted viruses in western Europe. Now, however, these ideas are changing. The possibility that eriophyid mites could have some connection with plant virus transmission was first suggested so long ago as 1927 by Amos *et al.* (1) and confirmed by Massee (2) in 1952. Then, virologists becoming mite-conscious, three more instances of mite transmission were discovered in quick succession [Slykhuis (3); Wilson Jones & Cochran (4); Flock & Wallace (5)]. Similarly with leafhopper-transmitted viruses in western Europe, after the initial discovery of *Rubus* stunt (6), two or three other instances of transmission by leafhoppers were soon described (7, 8). Two more examples of virus transmission by mandibulate insects have been recently recorded [Markham & Smith (9); Broadbent & Heathcote (10)]. At the present time, however, only one virus is known to be transmitted by thrips. We may anticipate, therefore, that with a more catholic conception of the general methods of plant virus transmission, other types of arthropod, or even nonarthropod, vectors may be added to the list. Recent reviews of the arthropod transmission of plant viruses have been contributed by Floyd Smith & Brierley (11) & by Smith (12, 13), and all the known vectors of plant viruses up to 1956 are listed in a book by Smith (14) published in 1957.

Types of Arthropods Concerned in Plant Virus Transmission

A study of the different kinds of arthropods that have so far been described as vectors of viruses shows a much greater proponderance in the Hemiptera, particularly the aphids. This may be partly due to the reasons

[1] The survey of the literature pertaining to this review was completed in April, 1957.

given in the preceding section and partly no doubt because the Hemiptera are, as a group, well suited by their feeding methods to act as vectors of viruses.

In the Hemiptera-Heteroptera there appear to be only two authentic cases of virus transmission, although there are many references in the literature to transmission by capsid bugs and other similar insects which have never been confirmed. The two cases of transmission by the Heteroptera which are apparently authentic are both by species of *Piesma*. *Piesma cinereum* Say is the vector of sugar beet savoy disease in North America [Coons, Kotila & Stewart (15)] and *Piesma quadrata* Fieber transmits the virus of sugar beet leaf crinkle in Germany [Nitsche & Forster (16)].

As regards the Hemiptera-Homoptera, of the 300 plant viruses so far known, about 90 are transmitted by aphids, and *Myzus persicae* (Sulzer) is outstanding in its ability to transmit more than 50 viruses. The aphid-borne viruses are of many different kinds; in addition to the more common mosaic-type viruses, ringspot, streak, and distorting viruses, such as those of potato leaf-roll and tobacco vein-distortion, are also transmitted by aphids.

Nine viruses are known to be transmitted by whiteflies (Aleurodidae); these viruses are mostly found in tropical countries and include diseases of cotton, tobacco, cassava, and *Abutilon*. Three white-fly-transmitted viruses which may be related strains are recorded from India where they affect *Dolichos*, beans, and *Hibiscus*.

The scale insects, Coccoidea, have so far been shown to transmit only one group of viruses all affecting the cocoa tree, *Cacao*, and causing "swollen shoot" and mosaic. Thirteen species are involved in the transmission of about seventeen different strains of virus.

The last of the Hemiptera-Homoptera, the leafhoppers, are implicated in the spread of a great many viruses, second only in number to those transmitted by aphids.

Of the leafhopper-type vectors, several species of lantern flies, Fulgoridae, transmit the viruses of corn mosaic, Fiji disease of sugar cane, mosaic of oats, and stripe disease of rice. Four species of the Cercopidae, frog-hoppers or spittle bugs, transmit the virus of alfalfa dwarf, also known as Pierce's disease of the grape.

The majority of the leafhopper vectors belong to the Jassidae and they transmit such well-known viruses as those of aster yellows, curlytop of sugar beet, potato yellow dwarf, cranberry false-blossom, peach yellows, and many others.

Among the recently discovered viruses transmitted by leafhoppers in western Europe may be mentioned that causing the disease of raspberry known as *Rubus* stunt, one or more of the viruses in cereals, strawberry green petal virus and an undescribed disease of *Lamium album* Linnaeus, the dead nettle (8a).

Several species of thrips, Thysanoptera, are concerned in virus trans-

mission; at the moment, however, only one virus is known to be spread by this type of vector. It causes spotted wilt of tomato and occurs under different names in many parts of the world.

Mandibulate insects have been shown to transmit two or three viruses. In the U.S.A. and Canada a mosaic of cowpea, *Vigna sinensis*, is spread by a beetle, *Ceratoma trifurcata* Forster, and a somewhat similar disease in Trinidad has another species of leaf beetle as a vector. In the United Kingdom and parts of Europe a disease of cruciferous crops known as turnip yellow mosaic is transmitted by various types of biting insects including beetles, grasshoppers, and earwigs [Markham & Smith (9)]. A somewhat similar disease also transmitted by beetles and known as turnip crinkle has recently been described (10).

As mentioned in an earlier paragraph several species of mites, Acarina, have now been incriminated as vectors of plant viruses. The species of mites and the virus diseases concerned are as follows, *Phytoptus ribis* (Westwood), the big-bud mite and reversion disease of black currants (1, 2); *Aceria tulipae* Keifer and wheat streak mosaic (3), *Aceria ficus* Cotte and fig mosaic (5) and a new species of mite *Eriophyes insidiosus* Keifer and Wilson and peach mosaic (4).

Different Relationships Between Viruses and Their Vectors

Mechanical transmission.—A certain amount of disagreement exists as to whether in fact there are any examples of mechanical transmission of plant viruses. The most authentic is probably that described by Walters (17); he fed a species of large grasshopper, *Melanoplus differentialis* (Thomas), on tobacco plants infected with mosaic and then transferred them immediately to healthy tobacco plants. He did the same experiment with tobacco ringspot and potato X viruses. In each case some positive transmissions resulted. Here we have, presumably, a purely passive transfer of infective sap from the jaws of the insect to the leaves of the healthy plants.

The situation as regards the transmission of certain aphid-borne viruses is not clear. These viruses are known as nonpersistent and are rapidly lost by the aphid vector and it has been suggested that infection of susceptible plants results from contamination with infective sap adhering to the mouthparts. Watson & Roberts (18) give a certain amount of evidence against the theory of mechanical transmission, emphasising the specificity of aphid vectors. Bradley (19) suggests that the ducts in the stylets may become clogged and the aphid, after moving to another plant, may inject this material when cleaning the stylets. Day & Irzykiewicz (20) consider that certain factors are conclusive of mechanical transmission. These are the short transmission cycle, the absence of a latent period, the rapid loss of the virus by the aphid, the ease with which the viruses can be transmitted mechanically and the absence of retention of virus following a moult. The question of the specificity of aphid vectors has still, however, to be explained, and Sylvester

(21) considers that vector specificity is due to factors dependent upon specific interactions among the viruses, the saliva of the aphids and the host plant cells being inoculated.

Perhaps the most direct evidence regarding the mechanism of virus transmission by aphids has been presented by Bradley and Ganong (19*a*). By irradiating various portions of the stylets of the green peach aphid with ultraviolet light, they demonstrated that transmissible virus is carried only on the tips of the stylets.

Nonpersistent and persistent aphid-borne viruses.—Broadly speaking there are two main types of aphid-borne viruses, depending on the time the virus is retained by the insect without recourse to a further source of infection. These types were named *nonpersistent* and *persistent* by Watson & Roberts (18), although there is no hard and fast dividing line between them. The efficiency of transmission of nonpersistent viruses is greatly affected by modifying the times of feeding and by starving the aphids before and after feeding. Thus the following are the main phenomena relating to the nonpersistent type of virus: (*a*) Vectors are optimally infective when they have fed for approximately 30 seconds on the infected plant. (*b*) Transmission is improved if aphid vectors are starved for a period before an infection (=acquisition) feed. (*c*) If aphids are starved after an acquisition feed they begin to lose ability to transmit within two min. (*d*) After acquisition-feeding infectivity is rapidly lost when the vectors feed on healthy plants. (*e*) Infectivity is lost much more slowly when the vectors fast after an acquisition-feed [Watson (22)].

With the persistent viruses, these modifications do not apply, although it is sometimes necessary for the aphid to feed on the source plant for some time in order to acquire the virus. This may be due in part to the fact that some at least of the persistent viruses are situated in the phloem which is not so readily accessible to the aphid. Once a persistent virus is acquired by the aphid, the insect remains infective for long periods, frequently for the rest of its life, without again having access to a source of virus.

Some other characteristics of aphid-borne persistent viruses differentiate them from the nonpersistent viruses. They are fewer in number [Anderson (23)] and as a rule are not transmissible by sap inoculation although the viruses of tobacco mottle and beet yellows can be transmitted mechanically, the latter with some difficulty. The specificity of aphid vectors seems more pronounced and there is frequently a delay in the development of infective power within the aphid after feeding on a source of virus. This delay, referred to as a "latent period," varies very much in the different viruses and may be a few hours or 10 to 19 days. The last period is exceptional and is discussed in a later section on the multiplication of plant viruses in their insect vectors.

Selective virus transmission by aphids.—From the fact of aphid specificity in virus transmission one form of selective transmission must naturally follow. For example, the two viruses of cauliflower mosaic and cabbage black

ringspot are both aphid-borne and occur commonly together in one plant. Certain aphid species such as *Myzus persicae* (Sulzer) and *Brevicoryne brassicae* (Linnaeus) will transmit both these viruses, but another aphid species, *Myzus ornatus* Laing, will transmit only the cauliflower mosaic virus leaving behind the cabbage black ringspot virus [Kvićala (24)]. Similarly, *Myzus ascalonicus* Doncaster will pick out cucumber mosaic virus from a complex of this virus and potato virus Y [Doncaster & Kassanis (25)].

Another type of selective transmission occurs when an aphid feeds upon a plant infected with two viruses, one of which has no insect vector. This is seen commonly in some potato virus diseases; potato rugose mosaic consists of the X and Y viruses and an aphid feeding on such a virus complex transmits only potato virus Y [Smith (26)]. Similarly from a plant infected with a mixture of cucumber and tobacco mosaic viruses the aphid will select out the cucumber mosaic virus.

There is another curious type of differential transmission where the aphid-transmissibility of one virus is governed by the presence in the same plant of a second virus. This is best seen in the complex virus disease of tobacco known as rosette; two components, the vein-distorting and mottle viruses, give rise to the disease. When both viruses are present together in the plant both are transmissible as persistent viruses by the aphid, *Myzus persicae.* However, if the viruses are separated and infect different plants then only the vein-distorting virus can be aphid-transmitted. No very convincing explanation of this phenomenon has yet been found. One case of differential transmission by a particular developmental form of an aphid has been described. The virus of hop mosaic is apparently only transmitted by the winged form of the aphid *Phorodon humuli* (Schrank) [Paine & Legg (27)].

Multiplication of plant viruses in their insect vectors.—That several of the leafhopper-borne viruses multiply in their vectors in now abundantly established and this question is discussed in a later paragraph. The evidence for such multiplication of virus in other insect vectors such as the aphids is at present very slight. Day (28) has carried out some experiments on the mechanism of transmission by aphids of potato leaf-roll which is a persistent virus. He considers that his results suggest that the virus multiplies to a limited extent within the aphid.

Day bases his conclusions on the following considerations: (*a*) The ability of the vector to transmit would be proportional to the duration of the acquisition feed in delayed mechanical transmission but would be unrelated in propagative transmission. Results with potato leaf-roll virus favour the second alternative. (*b*) The maximum efficiency of transmission should occur with shorter intervals between acquisition and transmission with delayed mechanical transmission but should increase with time in propagative transmission. The data obtained suggest the second alternative. (*c*) The frequency distributions of the number of infections plotted against the duration of the inoculation feeding period would follow a normal distribution curve if transmission was by the delayed mechanical transmission but would follow an

exponential curve with propagative transmission. In this too the data suggest the second alternative. On the other hand experiments performed by Cadman & Harrison, also on potato leaf-roll (29), provide no evidence of virus multiplication in the aphid. They wished to investigate the effects of high temperature on the persistence of the virus in *Myzus persicae*. The ability of infective aphids to transmit the virus was greatly decreased by exposing them at 32°C. for three or six days. The ability to transmit more regularly did not return when the aphids were kept for a further period at 20°C. These results do not support the theory of multiplication in the insect vector.

Slightly more convincing evidence is presented by the case of *Pentatrichopus fragefolii* (Cockerell) (= *Capitophorus fragariae* Theobald), the aphid vector of strawberry crinkle virus [Prentice (30)]. There appears to be a latent period of the virus in the aphid of at least four days which may be extended to as much as 10 days. This is the longest latent period recorded for any aphid-borne virus and suggests that multiplication of the virus may take place to account for such a long delay.

When we come to consider the leafhopper-borne viruses the evidence for virus multiplication within the vector is, in many cases, quite convincing. The earlier and more circumstantial evidence is derived from the inheritance of the virus by the progeny of viruliferous leafhoppers. Fukushi (31) was the first to demonstrate this by his work on the dwarf disease of rice and its vector *Nephotettix apicalis* Motschulsky. He showed that the virus could be passed through six generations of leafhoppers involving 82 leafhoppers and 1200 plants. This was all derived from a single viruliferous female without further access to a source of virus. Infection is passed only from the female and not the male parent. Black (32) has shown that the virus of clover club leaf is also inherited by the progeny of viruliferous females of the leafhopper *Agalliopsis novella* Say. The virus was passed through twenty-one generations over a period of five years without recourse to a further source of virus, the original virus-bearing female being mated to a virus-free male five years previously. It has been calculated that if no multiplication had taken place the dilution must have exceeded 10^{-26}.

Kunkel (33) investigated the question of the multiplication of the aster yellows virus in the leafhopper vector, *Macrosteles fascifrons* Stål, by subjecting viruliferous insects to varying temperatures. He found that the insects lost their ability to transmit the virus within 24 hr. of exposure to a temperature of 32°C. After one day's exposure at this temperature they regained infectivity in a few hours if returned to a temperature of 24°C. If kept for several days at the higher temperature, it required two days for them to regain infectivity and if kept for 12 days at 32°C. infectivity was lost altogether. Kunkel interpreted these results as indicating that the longer the insects were kept at a high temperature the more the virus concentration in the insect was reduced and in consequence a longer time was necessary for the virus to multiply up again to the level of an infective dose.

If heated too long all the virus was destroyed in the insect and infective power was lost until the insect fed once more on a source of virus.

A more direct approach was made to the problem by Maramorosch (34) who by means of a microsyringe injected the virus of aster yellows into leafhoppers in serial succession. He succeeded in carrying the virus through 10 groups of leafhoppers and calculated that if multiplication had not taken place the dilution would have reached 10^{-40}.

Finally, mention must be made of the method of measuring virus increase by means of insect tissue culture. Maramorosch (35) sterilized the surface of a number of viruliferous nymphs of *Macrosteles fascifrons* the vector of aster yellows. He then cut them up into small pieces in a solution containing antibiotics. The tissues were suspended for 10 days at 25°C. in hanging drops of a culture medium. They were then ground up in Ringer's solution, and inoculated into adult leafhoppers. Of 80 groups of three insects each, seven transmitted the virus after an incubation period of 28 to 38 days. No virus was recovered from insects ground up immediately after a two-day infection feeding. Since the virus completed its incubation period in vector tissue suspended in hanging drops the results suggest that it multiplied in these tissues.

Transmission by mandibulate insects.—The virus of turnip yellow mosaic (9) offers a good example of transmission by mandibulate insects. The natural vector is one or more species of flea beetles, *Phyllotreta*, but any species of beetle, including weevils, can transmit the virus. In addition to beetles, various types of other mandibulate insects such as grasshoppers, *Leptophyes* sp., *Stauroderus* sp., and earwigs (*Forficula auricularia* Linnaeus) have all transmitted the virus under experimental conditions. The main factor in successful transmission by all these insects appears to lie in regurgitation during feeding. Certain other biting insects such as caterpillars which do not regurgitate cannot transmit the virus. During the process of feeding the regurgitated fluid, containing the virus, is brought into contact with the leaf and infection is thus effected.

The exact relationship between this virus and the vector is not clear; it is probably more than a mechanical process since the beetles can retain infective power for seven days or longer. On the other hand it may be that retention of infectivity is entirely dependent on the time that viable virus remains in the foregut and can still be regurgitated. We know that the virus is extremely resistant to enzymic action, as it can be recovered in an infective condition from the faeces of snails and lepidopterous larvae which have fed on leaves infected with the turnip yellow mosaic virus. The virus is not retained over the winter in hibernating beetles nor does it pass from an infective beetle larva through the pupal stage to the adult. A more complex relationship is possible in the case of squash mosaic virus and its beetle vector. Freitag (36) has shown that the virus may be retained by the vector for 21 days. Moreover, active virus was recovered from the blood and faeces as well as from regurgitated fluid. Other examples of viruses with

mandibulate insect vectors are those of turnip crinkle (10) and cowpea mosaic (37).

Effect of viruses on their insect vectors.—It has for long been taken for granted that plant viruses have no deleterious or other effect upon their insect vectors. With the demonstration that some viruses multiply in their leafhopper vectors this view is likely to be modified. If a virus multiplies in a living cell there must be presumably some effect if only at a cellular level. From time to time various statements have been made on this subject. Dobroscky (38) failed to detect any histological difference between viruliferous and virus-free leafhoppers in the case of the aster yellows virus. Hartzell (39) stated that he had observed intracellular inclusions similar to those occurring in infected plants in the case of peach yellows and its vector *Macropsis trimaculata* Fitch, and Blattny (40) considered that there were changes in the salivary glands of aphids infected with potato leaf-roll virus. Neither of the last two observations have been confirmed.

In 1956 Littau & Maramorosch (41) made a comparative histological study with the optical microscope of viruliferous and virus-free aster leafhoppers (*Macrosteles fascifrons* Stål). They discovered an apparent difference, not in the salivary glands as might perhaps be expected, but in the fatbody. In nonviruliferous leafhoppers the nuclei tended to be rounded with homogeneous cytoplasm and the cells were intact. In viruliferous leafhoppers almost all the nuclei of the fatbody cells were stellate with reticulate cytoplasm. Many cells appeared abnormal and broken in sections. Littau & Maramorosch suggest that this is an indication of disease in the vector caused by multiplication of the aster yellows virus.

Some interesting experiments carried out by Kunkel (42) may be relevant to this question. Two strains of the aster yellows virus occur which differ slightly in host range but cause identical symptoms on their common hosts. Kunkel, however, was able to find two plants which could be used as differential hosts. These were *Vinca rosea* and *Nicotiana rustica* and by means of these he proved that aster yellows and California aster yellows viruses showed cross immunity. Furthermore he was able to show that an apparently similar cross-immunity existed in the leafhopper also. In every case when the insect was fed successively on the two strains, it transmitted only that on which it fed first. This suggests that certain cells, possibly of the fatbody, were occupied by the strain of virus first imbibed and this precluded, not necessarily the entrance, but probably multiplication, of the second virus strain.

Mutation of Viruses in Relation to Insect Transmission

It is probable that the attitude of plant virologists to the whole question of insect transmission will need some revision. The fact of insect-transmissibility of a given virus has been far too long regarded as a fixed property of the virus and there is considerable evidence already available that this is not the case. It is possible to find several instances where an insect-borne

virus loses this property either wholly or in part. Black (43) has described how three isolates of the virus of potato yellow dwarf were kept going in plants by mechanical transmission methods for periods of $16\frac{1}{2}$ and 12 yr. without contact with their leafhopper vectors. Using 450 leafhoppers in transmission experiments Black failed to obtain any infections. On the other hand 433 leafhoppers fed on a clover source plant infected with a fresh virus isolate produced 102 infections. From this it seems clear that the virus has lost its insect-transmissibility by reason of its long period out of contact with its insect vector. Other similar cases can be quoted, the well-known virus variegation in *Abutilon thompsonii* is apparently no longer transmissible by the whitefly *Bemisia tabaci* (Gennadius) which is the vector of the virus in other *Abutilon* spp. This is presumably due to the fact that *A. thompsonii* has for so long been propagated for its attractive variegation in European countries where the insect vector is not indigenous (44). Similarly there is some evidence of a change in aphid vector-relationship of a yellow strain of cucumber mosaic virus which has been maintained by mechanical transmission only for a period of 20 yr. (45).

These are changes in vector relationship which are presumably due to artificial separation of the virus from contact with its insect vector. There are other instances of loss of insect-transmissibility which are apparently caused by the infection of different or unusual host plants. Potato viruses Y and C are closely related strains of the same virus and while virus Y is aphid-borne, virus C is not so transmitted. However, Watson (46) has found a strain of the latter virus which is aphid-transmissible and moreover, this transmissibility is apparently reversible, being associated with passage through the potato variety Majestic. Because the insect-transmissibility is lost after passage of the potato, Watson suggests that the change is a qualitative one, the virus mutating from the potato strain to the *Nicotiana* strain while infecting *Nicotiana glutinosa*, the reverse mutation being induced by re-inoculation to potato.

It might be suggested therefore that there are at least three factors which may, individually or collectively, play a part in affecting the insect-transmissibility of a virus. These are: (*a*) artificial separation of a virus from its insect vector for a period of years; (*b*) unusual or unsuitable environment; and (*c*) particular or unusual species of host plants.

The recognition of the variability in the insect relationships of a virus enables us to suggest explanations for some of the unsolved problems of plant virology. The paracrinkle virus which is present in every plant of the potato variety King Edward has long been the subject of speculation (47). This virus appears to have no natural method of spread and has never been found occurring in the field in any other potato variety or plant. The problem is therefore to explain how the paracrinkle virus entered the original seedling of this potato variety. Some recent work by Kassanis (48) suggests a possible explanation. He has shown that there exists a serological relationship between the paracrinkle virus, another latent potato virus known

as virus S, and a latent virus from carnations; of these three only the last named is aphid-borne. The assumption we can make, therefore, is that the original King Edward potato seedling was infected by an aphid-borne virus from carnations; possibly the carnation latent virus or a similar one. Once in the potato plant, a mutation occurred by which the virus lost its insect transmissibility, and this may have been further fixed by the continued vegetative propagation by the tubers.

A somewhat similar case has been described by the writer (49). This is a plant of *Arabis hirsuta*, rock cress, originally infected with the virus of cabbage black ringspot and kept under observation in the glasshouse for a period of 21 yr. For the first five yr. or so tests made from the *Arabis* plant yielded only the cabbage black ringspot virus. However, during a period of very low temperature in December 1940 the symptom picture in the plant changed and in addition to the original virus a second virus was isolated. During the ensuing 15 yr. this second virus changed twice in various ways such as host range and slight alterations in the physical properties. In no case, however, were any of the viruses, other than that of the original cabbage black ringspot, aphid-transmissible.

The most likely explanation for this interesting phenomenon is similar to that put forward for potato paracrinkle virus, i.e., that the *Arabis* plant was accidentally infected by an aphid-borne virus, probably that of cucumber mosaic, and that during the long period under the artificial conditions of the glasshouse the virus lost its insect-transmissibility and also changed some of its other properties.

Factors Influencing the Spread of Insect-Borne Viruses

Host plant-virus relationships.—One combination of circumstances which can appropriately be discussed under this heading is the concentration of the virus in certain leaves and the availability of such leaves to aphids alighting on the plant.

There are two common nonpersistent viruses both transmitted by the aphid *Myzus persicae;* these are the cauliflower mosaic and cabbage black ringspot viruses and although the latter has a wider host range and occurs in higher concentration, the former is much more common in fields of cauliflowers. Broadbent (50) suggests that this may be partly accounted for by the fact that the cabbage black ringspot virus is localized in the old leaves of the plants whereas the cauliflower mosaic virus is concentrated in the new leaves. After flying, the aphids tend to alight on the upper parts of the plant and are thus more likely to acquire the cauliflower mosaic virus. In this connection also the reader is referred to some papers on the distribution of aphid infestation in relation to leaf age (51, 52).

The distribution of viruses in the different tissues of a leaf may also have some bearing on virus spread and on some of the anomalies of aphid transmission. Thus there is a relatively high concentration of some viruses in the epidermal cells together with an unequal distribution of extractable

virus in different tissues [Bawden, Hamlyn & Watson (53)]. It seems sometimes necessary for a virus to be acquired by an aphid vector from one tissue in the plant but to be injected into a different tissue for infection to follow. This may be the case with beet yellow net virus which can be acquired by the aphid in 5 min. but the inoculation threshold of which is 15 min. Sylvester (54) suggests that it may only be necessary to penetrate the mesophyll to acquire the virus but that the insect must reach the phloem for successful inoculation.

Occasionally the species of plant inoculated may influence the spread of a virus; thus, with the virus of mustard mosaic, one species of aphid transmits it more easily to mustard, while another is the more efficient vector to Chinese cabbage [Sylvester & Simons (55)].

Feeding habits of vectors.—The actual plant tissues penetrated by hemipterous vectors is of importance in the acquisition and spread of viruses. Thus in the case of some of the persistent aphid-borne viruses, such as that of potato leaf-roll and tobacco vein-distorting virus, it is probably necessary for the aphid to penetrate to the phloem to bring about infection. Similarly with curly-top of sugar beet, the leafhopper vector is a phloem feeder and cannot either transmit the virus or survive if it is unable to reach the phloem [Bennett (56)].

On the other hand in the case of the virus of alfalfa dwarf (Pierce's disease of the grape) the only leafhoppers which can act as vectors are those which are xylem feeders [Houston, Esau & Hewitt (57)].

We have seen with regard to the mandibulate vectors of turnip yellow mosaic virus that only those insects which regurgitate while feeding can transmit the virus and this seems to be the case with other viruses similarly transmitted (36).

Proximity of virus and vector sources.—The presence of a source both of virus and vector within the neighborhood of a susceptible crop is obviously going to influence the spread of the virus. There are many instances of this; it is unwise to have the potato seed crop near to peach trees since these are the hosts which carry the winter egg of the chief aphid vector of potato viruses, *Myzus persicae*. Similarly, annual leguminous crops such as peas and beans should not be grown in the vicinity of clover, since this harbours both the viruses which attack peas and beans and also the aphid vector. In Europe whenever feasible the beet seed crop should be grown as far as possible from the root crop since the mother beets are almost invariably infected with the viruses of mosaic and yellows and also harbour the aphid vector. A good example of how a susceptible crop can be kept free of virus by avoiding the insect vector is given by the Scotch seed potato industry. By confining the seed potato crop to areas of Scotland where the climate is unfavourable to *M. persicae*, it is possible to keep the seed potatoes free of insect-borne viruses; this cannot be done in England at present.

Movement of aphid vectors.—It has been shown (58) that the activity of aphids in a crop is far more important than numbers so that the compara-

tively few alate individuals play a greater part in the spread of virus than the large numbers of apterous aphids. As Kennedy (59) has pointed out, many workers have assumed that the migrant aphids sense and make their way towards their specific host plants from a distance. That this is not so has been pointed out by Heinze (60), Broadbent (61) and Kennedy (59). The last-named records how the autumn migrants of *M. persicae* were caught alighting quite indiscriminately on their specific winter host, peach, and on another tree, spindle, on which they do not over-winter. Thus the aphids exercised their selection between suitable and unsuitable hosts mainly after alighting on them.

The most important points therefore affecting the virus-spreading efficiency of a given aphid species are its ability to transmit the virus, and the abundance and activity of its winged forms, rather than its potentialities as a direct pest of the crop. In other words, the casual winged insect vector which may alight and feed on a plant before moving off again is a more important agent in the spread of a virus than the vector which alights and remains to colonize the crops (59).

Intrinsic properties of a virus in relation to transmission.—The low thermal inactivation point of some viruses may have a considerable influence on their spread in the field. For example during the summer months in the U.S.A., especially in the south, the leafhopper *Macrosteles fascifrons* (Stål) tends to lose its ability to transmit the virus of aster yellows either temporarily or permanently according to the length of the hot weather (62). It is interesting to speculate whether high temperatures may also play some part in the transmission of the tomato spotted wilt virus by thrips. Although the virus seems to spread easily enough in several tropical countries, it is sometimes extremely difficult to induce the thrips to transmit the virus under experimental conditions in the glasshouse and the thermal inactivation point is only 42°C.

The length of time an aphid-borne virus will remain infective within the vector will also influence its spread. In other words if the virus is of the persistent type, such as that of potato leaf-roll, it can be carried long distances by aphids drifting on the prevailing winds. Aphids can acquire and transmit leaf-roll virus only after feeding periods of some hours, and so spread within the crop is favoured by conditions which restrict flight. On the other hand a nonpersistent virus such as potato virus Y does not remain long infective in the aphid and so spreads mostly in calm, warm weather suitable for flight since aphids can make no headway against the mildest breeze (58).

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